THE SOCIAL AND SPATIAL BEHAVIOUR OF CARIBOU *RANGIFER TARANDUS*

by

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ABSTRACT

All animals are social at some point in their life. The causes and consequences of animal social behaviour are widely studied, but the integration of space use and spatial features of the landscape within our understanding of social behaviour is not widely studied. My thesis broadly addresses the role of spatial features of the landscape and individual-level space use traits as potential drivers of emergent social behaviour in caribou (*Rangifer tarandus*). First, I present a theoretical framework linking social and spatial behaviour within the context of evolutionary and behavioural ecology theory. Next, I assess the relationship between social behaviour and space use across scales, from fine-scale foraging and interactions to coarse-scale examination of how individuals and groups vary social behaviour through space and time. Overall, I found that caribou social behaviour is linked to space use and spatial behaviour in four important ways. First, I found that collective movement was an important predictor for patterns of habitat selection, where caribou tend to select foraging habitat (i.e. lichen) while alone, but to move collectively between foraging patches. Second, despite high home range overlap between caribou, and thus potential to associate, sub-groups of individuals had strong social preference for one another and formed distinct social communities. Third, based on a thirty year dataset of caribou group size, I found that group sizes varied spatially and temporally. In contrast to our expectation, groups decreased in size as a function of increasing population density, while groups tended to be larger in winter compared to summer, presumably as a result of seasonal access to foraging opportunities. Finally, I found that social network strength and habitat specialization were density-dependent, while more social individuals were habitat generalists. However, habitat specialization had a greater effect on fitness, where

habitat specialists had higher fitness than habitat generalists, but only at high density. My thesis addresses questions about the relationship between social and spatial behaviour and provides a theoretical framework for future studies to address similar questions. Throughout my thesis I also argue for the integration of various diverse ecological fields, including socioecology, spatial ecology, movement ecology, and conservation biology.

LAND ACKNOWLEDGEMENT

I respectfully acknowledge the territory where data were collected and analyzed as the ancestral homelands of the Mi'kmaq and Beothuk. I also recognize the Inuit of Nunatsiavut and NunatuKavut and the Innu of Nitassinan, and their ancestors, as the original people of Labrador. As a settler researcher working and living on stolen land I strive to understand the atrocities of the past and work towards building a respectful relationship with all people of this province as we search for collective healing and true reconciliation.

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I cannot thank the residents of Fogo Island enough for embracing me as a visitor to their island. Numerous residents of Fogo Island provided support in the field, but I

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DEDICATION

This thesis is dedicated to my family. Thanks for always supporting me.

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CHAPTER 1:INTRODUCTION AND OVERVIEW

1.1 Integrating social and spatial behaviour

In this section I present background information on the causes and consequences of animal sociality with respect to how social behaviour is related to space use.

1.1.1 The Causes and Consequences of Animal Sociality

All animals must engage in social interactions at some point during their lives (Frank 2007). Social interactions range from affiliative to agonistic, and the social phenotypes of individuals, populations, and species are highly flexible. These interactions are the product of genetic and environmental conditions that combine to influence fitness (Hofmann et al. 2014). Unlike many other phenotypes, the evolution of social behaviour is also influenced by the phenotypes (and sometimes genotypes) of other members of the same species (Wolf et al. 1998; Blumstein et al. 2010). Social behaviour and social groups are therefore highly dynamic. Behaviour is the interface between an animal and its environment; behaviour is therefore predicted to adapt relatively quickly compared to life-history or morphological traits (Kappeler et al. 2013). Indeed, social behaviour is no exception and is expected to adapt quickly, and often in an ideal free manner, to environmental variation, including variation in resources, competitors, mates, and predators (Tregenza 1995).

The social and physical environments therefore interact to influence social phenotypes (Webber and Vander Wal 2018). Fission-fusion societies are a manifestation of how variation in the social and physical environments influence patterns of individual social behaviour (Aureli et al. 2008). Fission-fusion occurs when members of the same group split (fission) and merge (fusion), often based on spatiotemporal variation in

resources (Couzin and Laidre 2009). The complexity of fission-fusion societies therefore represents a unique opportunity to study the effects of variation in the social and physical environments on individual behaviour. For example, social connections can be ephemeral and only exist for a short period of time, but some individuals also show long-term social stability and repeatedly interact over months or years (Chapter 3). Long-term stability of social groups is manifested as social preference among individuals. Social preference is the repeated, long-term association of two individuals, and individuals with social preference for one another may be more likely to remain together during fission. At a relatively fine-scale, individuals compete for foraging resources, and heightened competition could result in group fission.

Competition is cited as one of the primary costs of social behaviour (Alexander 1974). Various social and spatial mechanisms exist for animals to reduce the costs associated with competition, for example, individuals with strong social preference may preferentially forage together to reduce competition (Chapters 3 and 4). Familiar individuals are predicted to reduce competition with one another (Hasenjager and Dugatkin 2017). Thus, variation in the social and physical environment can influence the propensity for individuals to associate or develop social preference for one another. Apparent social associations could be masked by patchy distribution of resources, such as water-holes or other foraging resources, or features of the physical environment, such as mountains or rivers, and therefore forced to aggregate in groups based on this constraints (Chapter 3). Moreover, animal social groups exist in a spatial context, and, as the number of individuals in a group changes, the space occupied by that group is also expected to change (Chapter 5). As populations increase in size, the top-down effect of population

density on animal behaviour has become increasingly apparent, especially for social and spatial behaviours, which are often density-dependent (Chapters 2 and 6). The integration of social and spatial behaviour, and its effects on survival and reproduction, therefore has clear implications for the evolutionary ecology of animal social systems. This begs the question: what is the role of the physical environment in shaping the social environment?

1.1.2 Quantifying Social Behaviour using Social Network Analysis

Sociality is inherently hierarchical (Hinde 1976). Social interactions, defined as an action of one individual directed toward another or affecting the behaviour of another, are the finest scale of social behaviour (Whitehead 2008). Examples include affiliative interactions, such as allo-grooming, and agonistic interactions such as aggression. Importantly, for social interactions to occur, two animals must share space, indicating that variation in the physical environment those animals occupy can affect the type, frequency, or duration of social interaction. At the next scale, social association occurs when the social circumstances (e.g., range overlap or behavioural state) are those in which interactions usually take place (Whitehead 2008). For example, when two or more animals are in the same group, they are said to be associating (Franks et al. 2010). Social interactions and associations are therefore the foundation for social relationships among individuals and the structure of groups or populations. The highest level of social hierarchy is the social system, defined as groups of conspecifics that regularly interact more frequently with one another than with members of other groups (Whitehead 2008). Taken together, the structure, relationships, and interactions of a group of individuals form the social environment, which can be quantified as the size, sex ratio, or distribution of phenotypes within a group of interacting individuals.

Animal social network analysis has been used since the 1950s to quantify social relationships (for review see Krause et al. 2009) and gained popularity among behavioural ecologists in two last decades (Webber and Vander Wal 2019). The emergence of network analysis has honed our questions and provided new avenues to test hypotheses about the causes and consequences of complex animal social structures (Croft et al. 2011). As a result, animal social network analysis has become an important subdiscipline within behavioural ecology. Social dynamics, calculated using social network analysis, have been linked to a range of behavioural and ecological variables, including fitness (Stanton and Mann 2012; Vander Wal et al. 2015), movement (Spiegel et al. 2016), dominance (Bierbach et al. 2014), predation (Heathcote et al. 2017), animal personality (Wilson et al. 2013), information transfer (Firth et al. 2016), pathogen dynamics (Webber et al. 2016) and quantitative genetics (Fisher and McAdam 2017). Indeed, the application of social network analysis is widespread.

Use of animal social network analysis involves three primary steps (Farine and Whitehead 2015). First, information on social association or interaction is used to construct social networks. Animals can be observed interacting or associating (Altmann 1974), or association can be inferred with biologging technology (for examples see Croft et al. 2016). Second, social interaction or association data are converted into pairwise matrices and association indices are often calculated. This form of data conversion often involves correction of the data; for instance, heterogeneity in the number of observations per individual is corrected using the half-weight index (Cairns and Schwager 1987). Third, statistical or mathematical modelling of social networks is used to test hypotheses about underlying social network structure. For instance, individual or group-level social

network metrics may be generated and combined with attribute data (*sensu* Farine and Whitehead 2015). A wide range of social network metrics and association indices exist (for definitions see Wey et al. 2008; Silk et al. 2017), many of which are used as individual-based proxies for animal social interaction, or association and can be used in statistical models.

Although animal social network analysis is an important method for testing hypotheses about animal social structure (Croft et al. 2011), it is also relevant in an applied context (Makagon et al. 2012). Specifically, social network analysis has been used to quantify social structure for species of conservation concern, as well as for captive and domestic species. In a killer whale (*Orcinus orca*) network, targeted removal of key individuals can fragment social networks and potentially reduce cohesiveness of highly dynamic social units (Williams and Lusseau 2006). Moreover, social network analysis can also be used to predict pathogen dynamics (Drewe 2010; Rushmore et al. 2013), which can have implications for reservoir hosts of infectious disease (Hamede et al. 2012) or pathogen transmission from wild to domestic animals (Craft 2015). Social network analysis of captive or domestic species also provides an opportunity to improve animal welfare and husbandry practices (Rose and Croft 2015). Understanding social structure of captive and domestic species is important because many captive species are highly gregarious and housed in social groups while in captivity. For example, using social network analysis to quantify dominant–subordinate relationships between group members may be particularly important for captive species to reduce aggression and fighting (Makagon et al. 2012).

Social network analysis is a powerful tool for quantifying the social environment.

In Chapter 2, I discuss social networks as an important tool for quantifying social phenotypes in the context of animal space use and density dependence. When possible, I use social network analysis in this thesis to quantify and operationalize social associations (Chapters 3 and 6). In cases where I do not use social network analysis, it is because the data were collected blind to the identity of individuals (Chapter 4) or at the group level (Chapter 5).

1.2 Conservation Behaviour

1.2.1 Theory and Background

Wildlife conservation and management is being increasingly recognized as inter-disciplinary and incorporates aspects from a diverse range of disciplines including, but not limited to, physiology (Madliger et al. 2016), disease ecology (Smith et al. 2009), genetics and genomics (Allendorf et al. 2010), evolutionary ecology (Hendry et al. 2011), and animal behaviour (Blumstein 2010; Berger-Tal et al. 2016; Greggor et al. 2016). The field of conservation behaviour emerged from a call to integrate the previously disparate fields of conservation biology and animal behavioural ecology (Sutherland 1998; Caro 1999). When environmental conditions change, for example through anthropogenic disturbance or climate change, behavioural plasticity may be important adaptations for animals to cope with environmental change of change (Berger-Tal et al. 2011). Specifically, animal behaviour is a mediator between environmental change and population vital rates, which correspond to individual animals' probabilities of survival and reproductive success (hereafter, fitness). The link between behaviour and fitness, and the downstream consequences of changes in fitness (see Figure 2.1), are an important starting point for the field of conservation behaviour.

The integration of conservation biology and animal behaviour has evolved into the conceptual framework of conservation behaviour (Berger-Tal et al. 2011) that identifies specific behaviour-conservation links (Berger-Tal et al. 2016). The conservation behaviour framework outlines three themes linking conservation and behaviour: 1) direct and indirect anthropogenic impacts on animal behaviour; 2) behaviour-based management, including the use of behavioural ecology in conservation practice; 3) behavioural indicators of an animals state or the state of the environment (Berger-Tal et al. 2011). Therefore, the conservation behaviour framework requires knowledge of animal behaviour and, importantly, the conservation behaviour framework inherently assumes the adaptive nature of behaviour.

A scenario where behaviour might be important for conservation and management is through our understanding of density dependence. Many behaviours are density-dependent (e.g., Nicolaus et al. 2016; O'Brien et al. 2018), and if a given behaviour positively influences fitness, this behaviour could have an effect on population density. For example, individual-level social network traits can be density-dependent, wherein individuals become more socially connected as density increases (O'Brien et al. 2018; Webber and Vander Wal 2020). In such a density-dependent system, if more socially connected individuals have higher fitness (Aplin et al. 2015; Vander Wal et al. 2015), there are two outcomes. First, as density increases, individuals become more social. Second, as individuals become more social, the expectation is that fitness should increase, thus resulting in an increase in density through a feedback loop, or correlation. A potential outcome of this scenario is that the original behaviour may change due to density dependence (Webber and Vander Wal 2018). This type of feedback has been

observed for morphological and life-history phenotypes (Pelletier et al. 2007), but behavioural phenotypes also have potential to exist within such a feedback loop (Vander Wal and Webber 2020). Given that population density, abundance, and lambda (annual population growth) are important baseline parameters for conservation agencies, it is possible to envision a scenario where behaviour and conservation are integrated within an eco-evolutionary framework (Kinnison and Hairston 2007; Hendry et al. 2011). This hypothetical example highlights a potentially realistic link between behaviour and conservation. My application of the conservation behaviour framework therefore focuses on the behaviour → fitness → density → behaviour feedback loop.

1.2.2 Caribou Conservation Behaviour

Caribou are an iconic Canadian species. Active and inter-disciplinary research on caribou, including conservation behaviour, is required to inform policy and address the urgent need to conserve caribou in Canada (Serrouya et al. 2019; Harding et al. 2020; Johnson et al. 2020). Woodland caribou (*Rangifer tarandus caribou*) are federally listed as Threatened under the Canadian Species At Risk Act, while the Newfoundland sub-population is listed as Special Concern (COSEWIC 2014). Throughout their range in Canada, including Newfoundland, caribou populations are in decline (Bastille-Rousseau et al. 2013; Mallory and Boyce 2017).

As a result of their status as Threatened in Canada and Special Concern in Newfoundland, I think we have a moral obligation to frame all caribou research within a broader conservation context. As a behavioural ecologist interested in the causes and consequences of social behaviour, I ascribe to the conservation behaviour framework and the idea that a key element of behavioural ecology is the adaptive nature of behaviour

(Berger-Tal et al. 2011). My research priorities are based on the expectation that my results will, in some small way, inform caribou conservation. Two ways I link my research to conservation are through linking social behaviour to population dynamics and habitat selection. Specifically, caribou population density is known to fluctuate through space and time (Gunn 2003) and in my thesis I aim to demonstrate an understanding of how animal behaviour is linked to population dynamics and how changes in population density affect, and are affected by, animal behaviour (Chapters 2, 5, and 6). Furthermore, caribou declines in Newfoundland are related to density-dependent food limitation (Weir et al. 2014; Schaefer et al. 2016). I therefore address how social behaviour is related to foraging behaviour and habitat selection as a means to better understand the potential behavioural causes and consequences associated with food limitation (Chapters 3 and 4). In the next two sections, I present a broad overview of caribou natural history, conservation, and behaviour as the impetus and inspiration for my thesis.

1.3 Study Species and Study Area

In this section, I outline relevant background information on my study species and area; specifically, caribou herds in Newfoundland, as well as on Fogo Island. Due to the unique predator-prey relationships between caribou and their predators in Newfoundland, I also provide an overview of predator-prey dynamics of caribou in Newfoundland.

1.3.1 Newfoundland Caribou Herds

Newfoundland is an island off eastern Canada (47°44’ N, 52°38’ W to 51°44’ N, 59°28’ W) with a humid-continental climate and persistent precipitation throughout the year. There are 14 large caribou herds in Newfoundland (Bastille-Rousseau et al. 2013) as well as numerous smaller herds. For caribou, herds are typically defined as groups that exhibit

specific patterns of annual movements, which can include high fidelity to specific calving areas, typical patterns of distribution and movement for summer insect relief, seasonal migration, and wintering grounds (Schaefer and Mahoney 2013; Prichard et al. 2020). In addition to these herds, between the 1960s and 1980s the Government of Newfoundland and Labrador attempted at least 22 caribou translocations from herds in Newfoundland to islands or remote areas around the province (Bergerud and Mercer 1989). Although many of these translocations were unsuccessful, at least six of the translocated herds, including the Fogo Island herd, were successful (Bergerud and Mercer 1989).

Caribou herds in Newfoundland range in size from dozens of animals in the case of some of the introduced herds to over 10,000 animals in the case of the Middle Ridge Herd (Bergerud and Mercer 1989; Bastille-Rousseau et al. 2013). Most herds are partially migratory (Mahoney and Schaefer 2002) and females have relatively high philopatry to summer, but not winter, grounds (Schaefer and Mahoney 2013; Peignier et al. 2019). Among the larger herds, there is relatively little spatial overlap (Schaefer and Mahoney 2013) and inter-change of females between herds is uncommon (Bastille-Rousseau et al. 2013). As a result, most analyses (including those presented in Chapters 5 and 6) consider herds as distinct units.

Caribou forage primarily on lichen, grasses, sedges, and other deciduous browse (Bergerud 1974; Mahoney and Virgl 2003). Forage resources for caribou change between the seasons due to accessibility. During summer (July–September), the absence of snow yields relatively homogeneous distribution and higher abundance of vegetation, including grasses, sedges, and other deciduous plants, compared to winter, when caribou forage primarily on lichen (Schaefer et al. 2016). During winter (January–March), when the

landscape is covered by snow, access to vegetation becomes limited. To access forage in the winter, caribou dig holes in the snow, termed craters (Bergerud 1974). Caribou in Newfoundland tend to dig craters in locations where snow depth is relatively shallow (ca. 30–60 cm deep), such as hillsides or hummocks (Bergerud 1974). As a result, caribou cannot access all subnivean forage and tend to occupy and re-use craters once they are established. The average area of craters dug by caribou in Newfoundland was 0.41 m^2 (SD = 0.48; Mayor et al. 2009), and crater density, which varies based on snow condition, depth, and local caribou density, ranged from 366 to 1980 craters/ha (Pruitt Jr. 1959; Bergerud 1974); there is therefore considerably less access to forage than when the landscape is free of snow. The distribution of craters on the landscape is heterogeneous and access to vegetation in winter is highly variable.

1.3.2 Fogo Island Caribou

Fogo Island (237 km^2) is a small island located approximately 12 km off the northeastern coast of Newfoundland (49º40'0'' N, 54º11'0'' W); it has a humid climate with year-round precipitation. The dominant land types consist of coniferous and mixed forests of balsam fir (*Abies balsamea*), black spruce (*Picea mariana*) and white birch (*Betula papyrifera*), as well as bogs, lakes, and barren rock. Other habitat types include ponds, bog wetlands, lichen, and rocky barrens. Caribou on Fogo Island were introduced between 1964–1967 as one of 22 introductions across Newfoundland between 1961–1982 (Bergerud and Mercer 1989). The original introduction consisted of 26 individual caribou and the population has increased in size since then. Unlike many of the other herds in Newfoundland (Bastille-Rousseau et al. 2013), caribou on Fogo Island have experienced relatively stable population dynamics over the last two decades (Figure 1.1). Caribou on

Fogo Island are sedentary and do not display any migratory or long-distance movements.

Between 2016 and 2019, caribou were fitted with GPS collars, which were deployed on individuals for up to two years and in some cases, new collars were redeployed on caribou for an additional two years (for details see Chapter 3). Based on anecdotal evidence and mortality of GPS collared animals, there are a variety of causes of mortality for adult caribou on Fogo Island (Table 1.1). On Fogo Island, there is a four-week hunting season in October that includes 25 tags for either a male or female caribou (Government of Newfoundland and Labrador 2019). Based on our sub-sample of collared or tagged individuals between 2016 and 2019, only a single marked male caribou was shot (Table 1.1); however, during this time, I collected head or jaw bone specimens from fifteen hunted caribou (n = 6 males; n = 6 females; n = 3 unknown sex). In general, the removal of caribou due to hunting does not seem to be biased towards males or females. In addition to these various causes of mortality, anecdotal evidence suggests that caribou occasionally leave Fogo Island by swimming to the Island of Newfoundland. Although we have not recorded or observed dispersal to the Island of Newfoundland, caribou in our system are known to swim several kilometres in the Atlantic Ocean to other islands in the Fogo Island archipelago (Webber et al. *unpublished data*). I expect that dispersal via swimming is relatively rare and may only consist of a few animals each year, and that it therefore should not impact population dynamics. Population dynamics are therefore relatively stable and, as is the case for larger herds in Newfoundland, the limiting factors of population growth are likely calf predation and density-dependent food limitation (see below).

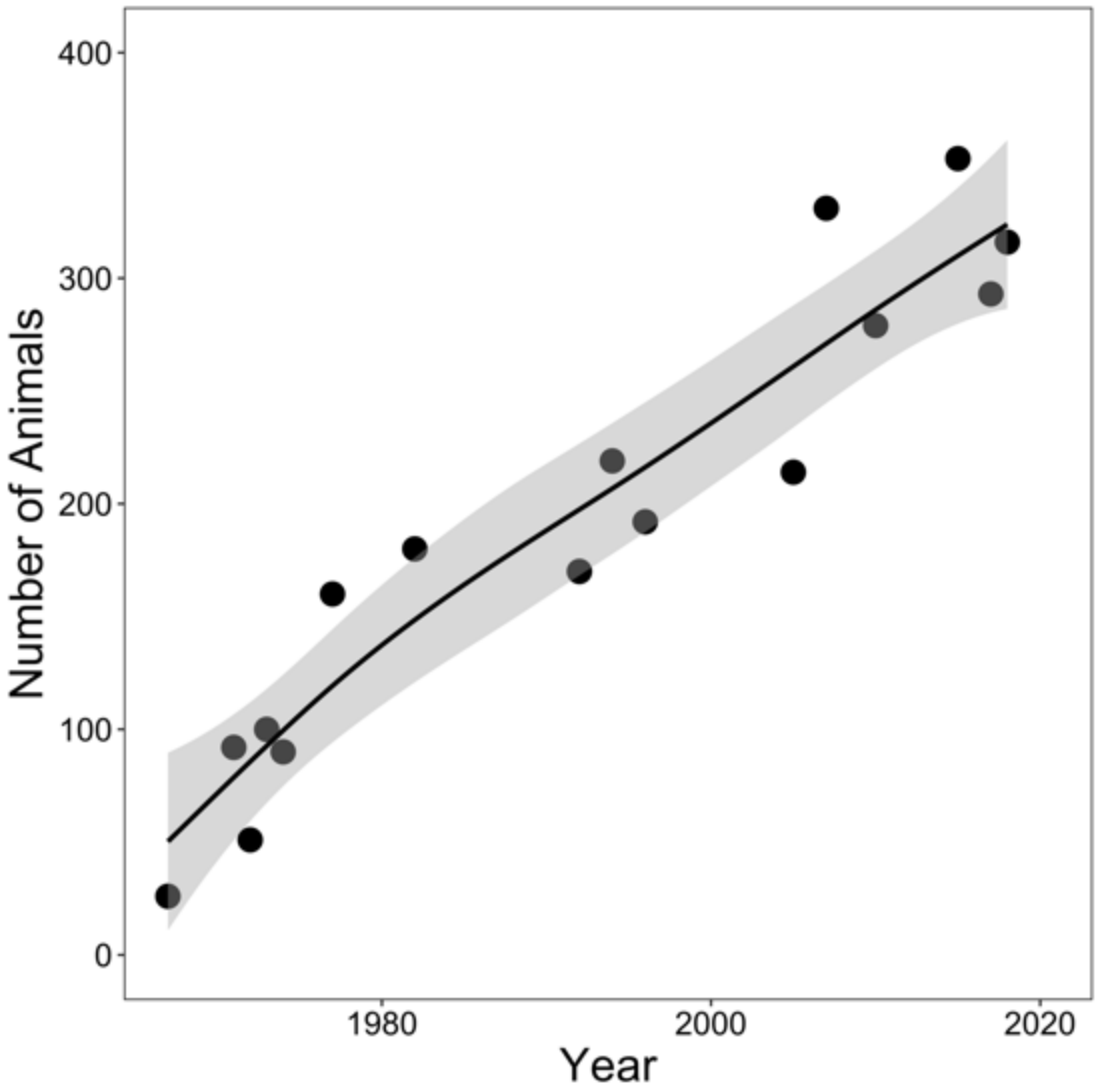

Figure 1.1: Number of animals in the Fogo Island caribou herd between 1967 and 2018 based on aerial surveys conducted by the Newfoundland and Labrador Wildlife Division. Trend line was fitted with a generalized additive model to account for non-linearity in the population trend and shaded grey area represents the 95% confidence interval around the trend line.

Table 1.1: Causes of mortality of tagged or collared adult caribou on Fogo Island between 2016 and 2020.

Cause of mortality	Number of deaths	
	Females	**Males**
Shot by hunter	4	1
Suspected brainworm	2	-
Died in parturition	1	-
Vehicle collision	1	-
Suspected predator	1	-
Unknown	1	-

1.3.3 Predators of Caribou

In Newfoundland, wolves (*Canis lupus*) were extirpated circa 1920 and coyotes (*Canis latrans*) and black bears (*Ursus americanus*) are now the primary predators of caribou (Bastille-Rousseau, Schaefer, et al. 2016). Coyotes and black bears are responsible for the majority of mortalities for neonate caribou calves (Bastille-Rousseau, Schaefer, et al. 2016), although predation can still occur after this period (Lewis and Mahoney 2014). Although predation by coyotes or black bears on adult female caribou is possible, it is relatively rare and the risk to adults is high; only ca. 6% of adult mortalities were attributed to predation (Lewis and Mahoney 2014). Coyotes underwent a natural range expansion into Newfoundland from Cape Breton, Nova Scotia, by crossing sea ice in approximately 1985 (McGrath 2004).

The first trapped coyote specimen from Fogo Island was submitted to the Newfoundland and Labrador Wildlife Division in April 2008 (Newfoundland and Labrador Wildlife Division, *unpublished data*), however, the colonization of Fogo Island by coyotes likely occurred prior to 2008. Unlike the Island of Newfoundland, there are no black bears on Fogo Island; coyotes are the only predator of caribou. Coyote density on Fogo Island remains unknown, but based on home range sizes for coyotes in Newfoundland (Fifield et al. 2013) and throughout their range (Ellington and Murray 2015), it is possible that Fogo Island (237km^2) could host as few as one (assuming ~300km^2 home ranges), but as many as seven (assuming ~35km^2 home ranges), breeding pairs of coyotes. A recent dietary analysis indicates that, similar to elsewhere in their range (Gompper 2002; McCue et al. 2014), coyotes on Fogo Island are dietary generalists (Huang 2019). Approximately 45% of coyote diet was composed of caribou specimens,

while 26% was snowshoe hare (*Lepus americanus*), 22% was voles (*Microtus sp.*), and 16% was plant materials (Huang 2019). Although caribou is the primary component of coyote diet, this study was unable to differentiate between adult and juvenile caribou (Huang 2019). In addition, resource selection analyses revealed that coyote and caribou spatially co-occur in the majority of habitats on Fogo Island (Huang 2019). These data on coyote diet and space use suggest that coyotes on Fogo Island represent a formidable predator that, although smaller than wolves, have potential to impact caribou population dynamics.

1.4 Caribou Conservation

In this section I highlight climate change and anthropogenic disturbance as drivers of population decline in woodland caribou. I discuss the broad implications of caribou declines related to anthropogenic disturbance, as well as highlight existing research on caribou declines related to anthropogenic disturbance in Newfoundland (COSEWIC 2014).

1.4.1 Fluctuations in Caribou Population Density

Fluctuations in animal population density are driven by a range of factors, including predation, competition, disease, and changes in regional or global climate. Caribou populations are no exception (Vors and Boyce 2009; Festa-Bianchet et al. 2011) and are predicted to fluctuate between synchronous phases of increase and decrease every 40 to 70 years (Gunn 2003). Within the Anthropocene, the natural fluctuations of many wildlife populations have been disrupted. For caribou, among the most important drivers of decline are climate change and anthropogenic disturbance (Vors and Boyce 2009), neither of which would have affected population dynamics historically. The effects of

climate change on caribou will be wide-ranging and include an increase in wildfire activity, an increase in summer insect harassment, mortality from parasites and diseases, changes in forage quality and quantity, increased rain and icing events in winter, changes to spring phenology, and changes in spatial distribution and migratory behaviour (for details see Mallory and Boyce 2017). Anthropogenic disturbance has also impacted population persistence and the spatial distribution of caribou populations (Vors et al. 2007).

In Newfoundland, as in the rest of their range, caribou population density has fluctuated over the last hundred years (Bergerud 1971; Bastille-Rousseau et al. 2013). In recent decades, the Newfoundland caribou population peaked in the 1980s and 1990s before a precipitous decline in the 2000s, followed by a current period of stability (Bastille-Rousseau et al. 2013). Several non-mutually exclusive explanations have been posited to explain population declines, including climate change induced predation (Bastille-Rousseau et al. 2016) and forage limitation (Schaefer et al. 2016).

1.4.2 Anthropogenic Disturbance

Anthropogenic disturbance has led to declines in caribou populations across North America (Bergerud 1974; Wittmer et al. 2005; Vors et al. 2007; Festa-Bianchet et al. 2011). Several non-mutually exclusive hypotheses have been proposed to explain caribou declines, although the most support exists for the disturbance-mediated apparent competition hypothesis. Specifically, disturbance-mediated apparent competition predicts that declines are the result of apparent competition between woodland caribou, moose (*Alces alces americanus*), and white-tailed deer (*Odocoileus virginianus*) as a result of heightened predation by wolves (*Canis lupus*) in disturbed landscapes (DeMars et al.

2019; Serrouya et al. 2019; Fryxell et al. 2020). Disturbance as a result of commercial logging (Beauchesne et al. 2014; Ewacha et al. 2017; Fryxell et al. 2020), wildfire (Joly et al. 2010; Lafontaine et al. 2019), and linear features (e.g. roads, hydro-lines, or seismic lines: Dickie et al. 2020) have a twofold effect on apparent competition. First, moose and white-tailed deer thrive in early successional forests following logging and wildfire, which supports an increased density of wolves. Second, linear features, such as roads, pipelines, railroads, and seismic lines facilitate predator search rates and access to caribou habitat (Dickie et al. 2017; Demars and Boutin 2018). Moreover, the presence of these anthropogenic disturbances can affect calf survival (Leclerc et al. 2014; Losier et al. 2015). Caribou therefore suffer from apparent competition when moose and white-tailed deer expand into caribou habitat, thus facilitating higher abundance of wolves.

Caribou typically require large tracts of mature coniferous forests and peatlands with relatively low densities of competitors and predators (James et al. 2004; Bowman et al. 2010). By contrast, moose tend to prefer early seral stages within the boreal forest, such as those that occur after commercial logging, wildfire, and other disturbances (DeMars et al. 2019). Predation risk for caribou could depend on the intensity of commercial logging and wildfire and the density of moose in a given area. Recent research in Ontario suggests that vital rates in areas with intensive commercial logging are lower than areas that had not experienced commercial logging, and risk of predation from wolves due to anthropogenic disturbance was sufficient to result in population declines (Fryxell et al. 2020).

Moose density in Newfoundland is relatively high, with abundance estimates ranging as high as150,000 animals in the 1990s (McLaren et al. 2004). As with elsewhere

in their range, moose in Newfoundland select early successional forests and can have significant impact on forest stands due to over-browsing (McLaren et al. 2000). Moreover, although anthropogenic disturbance in Newfoundland may be less intensive compared to Western Canada, commercial logging (Chubbs et al. 1993; Mahoney and Virgl 2003; Schaefer and Mahoney 2007; Hébert and Weladji 2013), mining (Weir et al. 2007), and hydroelectric development (Mahoney and Schaefer 2002) influence caribou habitat selection and movement. In the short-term, caribou tend to move away from anthropogenic disturbance (Chubbs et al. 1993; Schaefer and Mahoney 2007; Weir et al. 2007). The long-term consequences of these disturbances for caribou are a fragmented landscape and an increase in early successional forests, which are preferred by moose (McLaren et al. 2000). Although moose and caribou co-exist in Newfoundland, they tend to spatially segregate on the landscape (Mahoney and Virgl 2003). Furthermore, it is possible that disturbance-mediated apparent competition is related to caribou declines in Newfoundland. However, because there are no wolves in Newfoundland and coyotes are sub-optimal predators of moose and caribou, the effect of disturbance-mediated apparent competition is likely less than in areas where caribou coexist with wolves (COSEWIC 2014). In addition, the COSEWIC report on Newfoundland caribou notes that the role of apparent competition is unknown, but is not considered to be as significant as it is for other caribou populations in Canada (COSEWIC 2014). Caribou declines and the associated conservation and management is complex and often regionally distinct.

1.4.3 Caribou Declines in Newfoundland

The combination of relatively low anthropogenic disturbance in Newfoundland and lack of wolves suggests that disturbance mediated apparent competition is not responsible for

declines of Newfoundland caribou. The prevailing hypothesis explaining caribou declines in Newfoundland is twofold. Proximately, high levels of predator induced calf mortality is responsible for declines, but ultimately, density-dependent food limitation as a result of high population density led to smaller calves and greater vulnerability to predation (Weir et al. 2014; Bastille-Rousseau et al. 2016; Mahoney et al. 2016). Indeed, density-dependent food limitation resulted in pre-mature tooth ware (Schaefer et al. 2016), smaller body size (Mahoney et al. 2011), and altered space use (Schaefer and Mahoney 2013). The most recent caribou declines in Newfoundland ended around 2010 and early evidence suggests that most herds have stabilized since the end of the decline. While our understanding of the caribou declines in Newfoundland are well-studied from population and landscape ecology perspectives, the integration of behavioural ecology within this understanding is lacking. My thesis provides some insight into the causes and consequences of social processes during, and after, population declines.

1.5 A Seasonal View of Caribou Socioecology

Caribou and reindeer (*Rangifer tarandus*) live in loose fission-fusion societies (Body et al. 2015; Lesmerises et al. 2018), where groups merge and split through space and time. Groups vary in size throughout the year (Lesmerises et al. 2018) and are typically largest in winter and smallest in summer (Peignier et al. 2019). A potential explanation for variation in patterns of grouping is variation in food availability between summer and winter. As noted above, in winter, caribou dig holes in the snow (i.e. craters) and primarily forage on lichen (Bergerud 1974). Cratering locations may be limited due to the depth and hardness of snow (Bergerud 1974), so to cope with this limitation, caribou use

conspecific attraction and social information transfer to gain access to foraging opportunities (Peignier et al. 2019).

In contrast to winter, caribou aggregate in social groups during calving tend to be reduce the per capita risk of predation for calves. Specifically, caribou tend to have two social strategies during calving; aggregation or disaggregation (Bonar et al. 2020). In theory, aggregating in larger groups and giving birth synchronously swamps predators with a potential resource (i.e. vulnerable calves), thereby reducing the per capita risk. By contrast, disaggregating and giving birth alone reduces the likelihood of encountering predators and increases safety by occupying remote areas. In Newfoundland, caribou are known to use both strategies. In some of the larger herds, including Middle Ridge and La Poile, approximately 80% of the herd aggregate in large groups on calving grounds, while the other 20% of animals disaggregate and give birth solitarily (Fifield et al. 2012; Bonar et al. 2020). By contrast, in many of the other herds, including Fogo Island, all caribou disperse and give birth solitarily in remote areas (Webber *unpublished data*). The latter of these two strategies is most common among woodland caribou throughout their range; female caribou disperse to small islands (Bergerud and Page 1987), remote shorelines (Bergerud 1985), and rugged mountain slopes (Bergerud et al. 1984) to give birth. Dispersing to remote areas to give birth functions to avoid both predators as well as anthropogenic disturbance.

In summer, grouping patterns appear to be dictated by the availability of forage, which tends to be widely available. Specifically, in summer, caribou groups tend to be smaller, presumably because foraging opportunities are relatively abundant and also homogenously distributed on the landscape (Peignier et al. 2019). Near the end of the

summer, caribou tend to aggregate in smaller groups prior to the beginning of the rut. During the rut, caribou form loose harems where dominant males defend a small number of females against subordinate males (Body et al. 2014). In Newfoundland, the rut typically occurs in early to mid-October (Bergerud 1974). During the rut, male caribou form linear dominance hierarchies based on relative body and antler size (Barrette and Vandal 1990). Meanwhile, female hierarchies tend to be organized by body size and the presence or absence of antlers (Barrette and Vandal 1986; Hirotani 1990). After the rut, caribou aggregate in larger groups that remain relatively cohesive throughout the winter.

While caribou socioecology varies throughout the year, it also varies spatially. For example, group sizes for sedentary woodland caribou often do not exceed ten individuals (Jung et al. 2019), while group sizes for barren-ground caribou and arctic reindeer can exceed hundreds or even thousands of individuals (Witter et al. 2012). As a species, caribou ecotypes therefore tend to reduce group size as habitats become more closed, i.e., from open tundra to closed boreal forest.

Beyond a broad understanding of how caribou socioecology varies seasonally and between different ecotypes, little is known about the ecology and evolution of caribou social behaviour. Within my thesis, I quantify various social behaviours across spatial and temporal scales and assess how these behaviours vary as a function of environmental variation and influence fitness (see Section 1.6).

1.6 Thesis Narrative and Chapter Outlines

1.6.1 Thesis Narrative

Social traits occur at the individual-level but are complicated because one individual's social phenotype depends on one or more additional individuals. This is known as the

social environment. The prevailing narrative of my thesis research, and other research I have conducted in addition to my thesis, was to investigate the causes and consequences of the social environment as it varies through space and time. My broad objective was to invoke ecological and evolutionary theory, with underlying implications for conservation behaviour, to explain the causes and consequences of social behaviour (Chapter 2; Webber and Vander Wal 2018; Vander Wal and Webber 2020).

To lay the foundation for my thesis, I had two goals. My first goal was to develop a theoretical narrative linking social and spatial behaviour within the context of density dependence (Webber and Vander Wal 2018). Second, methods for generating social networks using GPS data were previously lacking and my goal was to develop methods to facilitate generating social networks using GPS data. Together with colleagues, I helped developed *spatsoc,* an R package that converts GPS relocations into social networks based on spatial distancing thresholds (Robitaille et al. 2019). Using these tools, we also examined the role of density dependence in shaping social network connections in elk in the context of consistent individual variation (O'Brien et al. 2018) and disease dynamics (Webber and Vander Wal 2020), as well as the role of seasonally variable habitats as a driver of social phenotypes in caribou (Peignier et al. 2019). Although these studies were primarily led by collaborators and mentees, they are inter-twined with my thesis because they represent foundational methods and theories on which my work is based.

The core narrative of my thesis is to demonstrate the theoretical and empirical links between the social and ecological environments. In Chapter 2, I outline the theoretical basis for our understanding of how density-dependent social and spatial

behaviours are linked and how these behaviours might affect fitness (Webber and Vander Wal 2018). I invoke theory on density-dependent habitat selection and the Ideal Free Distribution (Fretwell and Lucas 1969; Morris 2003), and build on this theoretical framework by incorporating theory on the evolution of social behaviour. My subsequent chapters fit within this broad theoretical framework.

For nearly all social interactions to occur, animals are required to either be moving towards, or with, conspecifics. In addition, movement is the underlying behaviour driving an animal's ability to search for, locate, and consume food through the process of habitat selection. Movement is therefore the proximate mechanism driving social interactions and foraging behaviour. In Chapter 3, I assess the role of movement and social network traits as potential drivers of habitat selection and foraging behaviour. Chapter 3 is an integration of social behaviour and movement ecology, a discipline I knew little about at the beginning of my PhD and originally had little intention of incorporating into my thesis. As I learned some of the novel analyses I used in other chapters (e.g., resource selection functions in Chapter 6), it became apparent that movement and habitat selection were inherently linked and to understand one discipline I had to understand the other. Late in my PhD I pivoted my thesis to incorporate a chapter on the influence of social behaviour and movement ecology (i.e. collective movement) on patterns of space use and habitat selection. Although Chapter 3 was not originally part of my thesis narrative, movement ecology fits within the socioecological framework outlined in Chapter 2 as the proximate mechanism driving fission-fusion dynamics and, as I argue, is the interface between social and spatial phenotypes.

At its finest scale, social behaviour is direct animal-to-animal interaction. Social interactions are highly variable, ranging from affiliative (e.g., allo-grooming) to agonistic (e.g., aggression), and occur in a variety of social and ecological contexts. In Chapter 4, I quantify aggressive interactions in the context of competition for resources for females and harassment of females by males. I assess how these interactions vary as a function of the social (group size and sex ratio) and physical (habitat types) environments. Chapter 4 fulfills several important goals of my PhD narrative. Specifically, as I had the opportunity to use existing data (Chapters 5 and 6) as well as remotely collected data (Chapters 3 and 6), my intention from the beginning of my PhD was to also have a chapter where I was entirely responsible for data collection. I designed data collection protocols and collected all data in Chapter 4. In addition, my intention for Chapter 4 was to fit within the finest scale of the socioecological framework outlined in Chapter 2. That is, I was interested in testing hypotheses about how the physical environment influences fine-scale social interactions.

For fission-fusion societies, animal groups merge and split through space and time. Groups are therefore expected to vary in size depending on social and ecological contexts. In Chapter 5, I assess variation in caribou group size as a function of habitat types, seasons, and population density. General questions in evolutionary ecology sometimes require large and long-term datasets to answer them. Chapter 5 uses a 30-year dataset of caribou group size and population density data to assess the potential for spatial, temporal, and density dependence of group size in Newfoundland caribou herds. While this dataset has been widely used to model population dynamics of caribou, the potential for density dependence of group size was unstudied. To complement this

dataset, I collected caribou group size data on Fogo Island for three years, an opportunity where I thought it would be important to contribute to an existing dataset. At its core, Chapter 5 is relatively straightforward, but it extends beyond Chapters 3 and 4 by incorporating concepts of density dependence, and fits broadly within the socioecological framework as a test of density dependence.

Social behaviour and habitat selection are density-dependent and their adaptive value is well established in theory and in practice. However, the link between social behaviour and habitat selection as individual phenotypes, and their potential to jointly impact fitness, remains untested. In Chapter 6, I quantify social network centrality and habitat specialization as individually-based phenotypes and assess their effects on reproductive success. I also assess the potential for these traits to display within- and between-individual consistency and to vary as a function of changes in population density. Most classic ecological theories omit to the identity of individuals. In this chapter, I bridge Ideal Free Distribution and Optimal Foraging Theories with our understanding of within- and between-individual variation in social and spatial behaviours. Chapter 6 represents the biggest and most holistic test of the socioecological framework proposed in Chapter 2. Specifically, in Chapter 6, I empirically test the predictions presented Box 2.1 in Chapter 2. By linking social and spatial behaviour within the Ideal Free and Optimal Foraging frameworks, we learn about the tension between being social and specializing on high quality habitat.

1.6.2 A Note on Citations of Recently Retracted Papers

Between January and September 2020 a number of articles cited in my thesis Chapter 2 (Webber and Vander Wal 2018) were retracted or had corrections issued. For all

unpublished chapters, I removed citations to articles that have been retracted during this period. However, Chapter 2 was written in 2016–2017 and published in 2018, which was prior to the retraction of any cited papers. As a result, I have decided to leave the citations to retracted papers in my thesis, as they are in the published version of this chapter.

Specifically, in Chapter 2, I cite five papers where the validity of data and the associated conclusions were brought into question. Of these five papers, three have been retracted (Laskowski et al. 2014; Laskowski and Pruitt 2014; Laskowski et al. 2020), one has undergone an authorship removal correction (Pruitt et al. 2016), while no issues have been reported for the final paper (Pruitt et al. 2017). In addition to disclosing these citations here, I have also modified the text of this thesis chapter to cite the retraction notices alongside the original papers. I have chosen to identify these citations and disclose why I chose to leave them in Chapter 2. In all cases, the original intention of the statements associated with those citations was largely theoretical and a citation of the ideas or definitions proposed in the retracted papers. However, given the lack of confidence in the data, I wish to acknowledge their retraction.

As an early career researcher who has witnessed these retractions happen in real time, it is now clear to me that open and transparent science is the only option, so I have posted all code and data to public online repositories. In some cases, the spatial locations of caribou are sensitive and data were not mine to post to public repositories, so in these cases I have posted derived data that were used for statistical analysis and to make figures.

1.7 Co-Authorship Statement

This thesis is the result of a PhD project in the Cognitive and Behavioural Ecology Interdisciplinary Program at Memorial University of Newfoundland. I am the major intellectual contributor and principal author of all chapters in this thesis. Data used in this thesis came from two primary sources. First, I used data collected and maintained through a long-term caribou monitoring program managed by the Newfoundland and Labrador Wildlife Division (NLWD) and the Sustainable Development and Strategic Science (SDSS) Branch of the Department of Environment and Conservation (now defunct). In Chapter 5, I used caribou herd composition data collected during aerial surveys by the NLWD between 1987–2013. In Chapter 6, I used a caribou GPS telemetry dataset collected by the SDSS between 2007–2013. Second, I collected data on caribou behavioural ecology on Fogo Island. All GPS telemetry data collected on Fogo Island were facilitated and supported by the NLWD (these data are presented in Chapter 3). I collected all data presented in Chapter 4. Acknowledgement to these sources is made within each thesis chapter.

I am responsible for all data analysis, interpretation, and manuscript preparation. The work would not have been possible without the collaborative contributions of many people, particularly my supervisor Dr. Eric Vander Wal and my co-authors on Chapter 6, Mike Laforge and Maegwin Bonar, and my co-authors on Chapter 3, Christina Prokopenko and Katrien Kingdon. I prepared the manuscripts and revised them based on the advice and comments from co-authors, reviewers, and colleagues. Beyond contributions of co-authors, acknowledgements are made at the end of each thesis chapter.

Chapter 1. Part of Section 1.1.2 Social Network Analysis has been published in *Animal Behaviour*.

Webber QMR, Vander Wal E (2019) Trends and perspectives on the use of social network analysis in behavioural ecology: a bibliometric approach. *Animal Behaviour*. 149:77-87.

Chapter 2. Webber QMR, Vander Wal E. An evolutionary framework outlining the integration of individual social and spatial ecology, has been published in *Journal of Animal Ecology*.

Webber QMR, Vander Wal E (2018) An evolutionary framework outlining the integration of individual social and spatial ecology. *Journal of Animal Ecology*. 87:113-127.

Chapter 3. Webber QMR, Prokopenko CM, Kingdon, K, Vander Wal E. Moving together, foraging apart: effects of the social environment on movement integrated habitat selection will be submitted to *Proceedings of the Royal Society B*.

Chapter 4. Webber QMR, Vander Wal E. Aggression in caribou: limited evidence for interference competition but strong evidence for male harassment will be submitted to *Ethology*.

Chapter 5. Webber QMR, Vander Wal E. Context-dependent group size: effects of population density, habitat, and season has been submitted to *Behavioral Ecology*.

Chapter 6. Webber QMR, Laforge MP, Bonar M, Vander Wal E. The adaptive value of density-dependent habitat specialization and social network centrality will be submitted to *Ecology Letters.*

1.8 References

Alexander RD. 1974. The evolution of social behavior. Annu Rev Ecol Evol Syst. 5(1):325–383.

Allendorf FW, Hohenlohe PA, Luikart G. 2010. Genomics and the future of conservation genetics. Nat Rev Genet. 11(10):697–709. doi:10.1038/nrg2844.

Altmann J. 1974. Observational study of behavior: Sampling methods. Behaviour. 49(3):227–267.

Aplin LM, Firth JA, Farine DR, Voelkl B, Crates RA, Culina A, Garroway CJ, Hinde CA, Kidd LR, Psorakis I, et al. 2015. Consistent individual differences in the social phenotypes of wild great tits, *Parus major*. Anim Behav. 108:117–127. doi:10.1016/j.anbehav.2015.07.016.

Aureli F, Schaffner CM, Boesch C, Bearder SK, Call J, Chapman CA, Connor R, Di Fiore A, Dunbar RIM, Henzi SP, et al. 2008. Fission-fusion dynamics: New research frameworks. Curr Anthropol. 49:627–654. doi:10.1086/586708.

Barrette C, Vandal D. 1986. Social rank, dominance, antler size, and access to food in snow-bound wild woodland caribou. Behaviour. 97(1):118–145.

Barrette C, Vandal D. 1990. Sparring, relative antler size, and assessment in male caribou. Behav Ecol Sociobiol. 26(6):383–387.

Bastille-Rousseau G, Schaefer JA, Lewis KP, Mumma MA, Ellington EH, Rayl ND, Mahoney SP, Pouliot D, Murray DL. 2016. Phase-dependent climate-predator interactions explain three decades of variation in neonatal caribou survival. J Anim Ecol. 85(2):445–456. doi:10.1111/1365-2656.12466.

Bastille-Rousseau G, Schaefer JA, Mahoney SP, Murray DL. 2013. Population decline in semi-migratory caribou (Rangifer tarandus): intrinsic or extrinsic drivers? Can J Zool. 91(11):820–828. doi:doi:10.1139/cjz-2013-0154.

Beauchesne D, Jaeger JAG, St-Laurent M-H. 2014. Thresholds in the capacity of boreal caribou to cope with cumulative disturbances: Evidence from space use patterns. Biol Conserv. 172:190–199. doi:10.1016/j.biocon.2014.03.002.

Berger-Tal O, Blumstein DT, Carroll S, Fisher RN, Mesnick SL, Owen MA, Saltz D, St. Claire CC, Swaisgood RR. 2016. A systematic survey of the integration of animal behavior into conservation. Conserv Biol. 30(4):744–753. doi:10.1111/cobi.12654.

Berger-Tal O, Polak T, Oron A, Lubin Y, Kotler BP, Saltz D. 2011. Integrating animal behavior and conservation biology: A conceptual framework. Behav Ecol. 22(2):236–

239. doi:10.1093/beheco/arq224.

Bergerud AT. 1971. The population dynamics of Newfoundland caribou. Wildl Monogr.(25):3–55.

Bergerud A.T. 1974. Relative abundance of food in winter for Newfoundland caribou. Oikos. 25(3):379–387.

Bergerud Arthur T. 1974. Decline of Caribou in North America Following Settlement. J Wildl Manage. 38(4):757. doi:10.2307/3800042.

Bergerud A T. 1974. Rutting behaviour of Newfoundland caribou. Behav ungulates its Relat to Manag. 1(20):395–435.

Bergerud AT. 1985. Antipredator strategies of caribou: dispersion along shorelines. Can J Zool. 63(6):1324–1329. doi:10.1139/z85-199.

Bergerud AT, Butler HE, Miller DR. 1984. Antipredator tactics of calving caribou: dispersion in mountains. Can J Zool. 62(8):1566–1575. doi:10.1139/z84-229.

Bergerud AT, Mercer WE. 1989. Caribou introductions in eastern North America. Wildl Soc Bull. 17(2):111–120.

Bergerud AT, Page RE. 1987. Displacement and dispersion of parturient caribou at calving as antipredator tactics. Can J Zool. 65(7):1597–1606. doi:10.1139/z87-249.

Bierbach D, Oster S, Jourdan J, Arias-Rodriguez L, Krause J, Wilson ADM, Plath M. 2014. Social network analysis resolves temporal dynamics of male dominance relationships. Behav Ecol Sociobiol. 68(6):935–945. doi:10.1007/s00265-014-1706-y.

Blumstein DT. 2010. Social behaviour in conservation. Soc Behav.:520–534. doi:10.1017/CBO9780511781360.041.

Blumstein DT, Ebensperger LA, Hayes LD, Vasquez RA, Ahern TH, Burger JR, Dolezal AG, Dosmann A, González-Mariscal G, Harris B, et al. 2010. Toward an integrative understanding of social behavior: new models and new opportunities. Front Behav Neurosci. 4(34):1–9. doi:10.3389/fnbeh.2010.00034.

Body G, Weladji RB, Holand O, Nieminen M. 2015. Fission-fusion group dynamics in reindeer reveal an increase of cohesiveness at the beginning of the peak rut. Acta Ethol. 18(2):101–110. doi:10.1007/s10211-014-0190-8.

Body G, Weladji RB, Holand Ø, Nieminen M. 2014. Highly competitive reindeer males control female behavior during the rut. PLoS One. 9(4):e95618. doi:10.1371/journal.pone.0095618.

Bonar M, Ellington EH, Lewis KP, Vander Wal E. 2018. Implementing a novel movement-based approach to inferring parturition and neonate calf survival. PLoS One. 13:e0192204.

Bonar M, Lewis K, Webber QMR, Dobbin M, Laforge MP, Vander Wal E. 2020. Geometry of the ideal free distribution: individual behavioural variation and annual reproductive success in aggregations of a social ungulate. Ecol Lett. 23(9):1360–1369. doi:10.1111/ele.13563.

Bowman J, Ray JC, Magoun AJ, Johnson DS, Neil Dawson F. 2010. Roads, logging, and the large-mammal community of an eastern Canadian boreal forest. Can J Zool. 88(5):454–467. doi:10.1139/Z10-019.

Cairns SJ, Schwager SJ. 1987. A comparison of association indices. Anim Behav. 35:1454–1469.

Caro T. 1999. The behaviour – conservation interface. Trends Ecol Evol. 14(9):366–369. doi:10.1016/S0169-5347(99)01663-8.

Chubbs TE, Keith LB, Mahoney SP, McGrath MJ. 1993. Responses of woodland caribou (*Rangifer tarandus caribou*) to clear-cutting in east-central Newfoundland. Can Jounal Zool. 71:487–493.

COSEWIC. 2014. COSEWIC assessment and status report on the Caribou (Rangifer tarandus) in Canada. :135.

Couzin ID, Laidre ME. 2009. Quick guide fission–fusion populations. Curr Biol. 19(15):633–635.

Craft ME. 2015. Infectious disease transmission and contact networks in wildlife and livestock. Philos Trans R Soc London Ser B, Biol Xciences. 370(1669):1–12. doi:10.1098/rstb.2014.0107.

Croft DP, Darden SK, Wey TW. 2016. Current directions in animal social networks. Curr Opin Behav Sci. 12:52–58. doi:10.1016/j.cobeha.2016.09.001.

Croft DP, Madden JR, Franks DW, James R. 2011. Hypothesis testing in animal social networks. Trends Ecol Evol. 26(10):502–507. doi:10.1016/j.tree.2011.05.012.

Demars CA, Boutin S. 2018. Nowhere to hide: Effects of linear features on predator–prey dynamics in a large mammal system. J Anim Ecol. 87:274–284. doi:10.1111/1365-2656.12760.

DeMars CA, Serrouya R, Mumma MA, Gillingham MP, McNay RS, Boutin S. 2019. Moose, caribou, and fire: have we got it right yet? Can J Zool. 879(June):866–879. doi:10.1139/cjz-2018-0319.

Dickie M, McNay RS, Sutherland GD, Cody M, Avgar T. 2020. Corridors or risk? Movement along, and use of, linear features vary predictably among large mammal predator and prey species. J Anim Ecol. 89(2):623–634. doi:10.1111/1365-2656.13130.

Dickie M, Serrouya R, DeMars C, Cranston J, Boutin S. 2017. Evaluating functional recovery of habitat for threatened woodland caribou. Ecosphere. 8:1–15. doi:10.1002/ecs2.1936.

Drewe JA. 2010. Who infects whom? Social networks and tuberculosis transmission in wild meerkats. Proc R Soc B. 277(1681):633–42. doi:10.1098/rspb.2009.1775. [accessed 2013 May 31]. http://www.pubmedcentral.nih.gov/articlerender.fcgi?artid=2842696&tool=pmcentrez&rendertype=abstract.

Ellington EH, Murray DL. 2015. Influence of hybridization on animal space use: A case study using coyote range expansion. Oikos. 124(5):535–542. doi:10.1111/oik.01824.

Ewacha MVA, Roth JD, Anderson WG, Brannen DC, Dupont DLJ. 2017. Disturbance and chronic levels of cortisol in boreal woodland caribou. J Wildl Manage. 81(7):1266–1275. doi:10.1002/jwmg.21288.

Farine DR, Whitehead H. 2015. Constructing, conducting and interpreting animal social network analysis. J Anim Ecol. 84:1144–1163. doi:10.1111/1365-2656.12418.

Festa-Bianchet M, Ray JC, Boutin S, Côté SD, Gunn A. 2011. Conservation of caribou (*Rangifer tarandus*) in Canada: an uncertain future. Can Jounal Zool. 434(5):419–434. doi:10.1139/Z11-025.

Fifield DA, Lewis KP, Gullage SE. 2012. Application of distance sampling to determine calving ground abundance and aggregation of parturient females in the Middle Ridge herd, June 2012. Tech Bull No 005, Sustain Dev Strateg Sci Gov Newfoundl Labrador, St John's, NL.

Fifield DA, Unger K, Lewis KP, Gullage SE, Mahoney SP. 2013. Spatial ecology of black bear (*Ursus americanus*), coyote (*Canis latrans*), and lynx (*Lynx canadensis*) in Newfoundland. Tech Bull No 007, Sustain Dev Strateg Sci Gov Newfoundl Labrador, St John's, NL.

Firth JA, Sheldon BC, Farine DR. 2016. Pathways of information transmission among wild songbirds follow experimentally imposed changes in social foraging structure. Biol Lett. 12(6):20160144. doi:10.1098/rsbl.2016.0144.

Fisher DN, McAdam AG. 2017. Social traits, social networks and evolutionary biology. J Evol Biol. 30:2088–2103. doi:10.1111/jeb.13195.

Frank SA. 2007. All of life is social. Curr Biol. 17(16):648–650.

Franks DW, Ruxton GD, James R. 2010. Sampling animal association networks with the gambit of the group. Behav Ecol Sociobiol. 64(3):493–503. doi:10.1007/s00265-009-0865-8.

Fretwell SD, Lucas HLJ. 1969. On territorial behaviour and other factors influencing habitat distribution in birds. Acta Biotheor. 19(1):16–36. doi:10.1007/BF01601953.

Fryxell JM, Avgar TAL, Liu B, Baker JA, Rodgers AR, Shuter J, Thompson IAND, Reid DEB, Kittle AM, Mosser A, et al. 2020. Anthropogenic Disturbance and Population Viability of Woodland Caribou in Ontario. J Wildl Manage. In Press:1–15. doi:10.1002/jwmg.21829.

Gompper ME. 2002. Top Carnivores in the Suburbs? Ecological and Conservation Issues Raised by Colonization of North eastern North America by Coyotes. Bioscience. 52(2):185. doi:10.1641/0006-3568(2002)052[0185:tcitse]2.0.co;2.

Government of Newfoundland and Labrador. 2019. 2019-2020 Hunting and Trapping Guide.

Greggor AL, Berger-Tal O, Blumstein DT, Angeloni L, Bessa-Gomes C, Blackwell BF, Cassady-St. Clair C, Crooks K, Silva S de, Fernández-Juricic E, et al. 2016. Research priorities from animal behaviour for maximising conservation progress. Trends Ecol Evol. 31(12):953–964.

Gunn A. 2003. Voles, lemmings and caribou - population cycles revisited? Rangifer. 23(5):105. doi:10.7557/2.23.5.1689.

Hamede R, Bashford J, Jones M, McCallum H. 2012. Simulating devil facial tumour disease outbreaks across empirically derived contact networks. J Appl Ecol. 49(2):447–456. doi:10.1111/j.1365-2664.2011.02103.x.

Harding LE, Spribille T, Wagner V, Darimont C. 2020. No statistical support for wolf control and maternal penning as conservation measures for endangered mountain caribou. Biodivers Conserv. 0123456789. doi:10.1007/s10531-020-02008-3.

Hasenjager MJ, Dugatkin LA. 2017. Familiarity affects network structure and information flow in guppy (*Poecilia reticulata*) shoals. Behav Ecol. 28:233–242. doi:10.1093/beheco/arw152.

Heathcote RJP, Darden SK, Franks DW, Ramnarine IW, Croft DP. 2017. Fear of predation drives stable and differentiated social relationships in guppies. Sci Rep. 7(February):41679. doi:10.1038/srep41679.

Hébert I, Weladji RB. 2013. The use of coniferous forests and cutovers by Newfoundland woodland caribou. For Ecol Manage. 291:318–325. doi:10.1016/j.foreco.2012.11.011.

Hendry AP, Kinnison MT, Heino M, Day T, Smith TB, Fitt G, Bergstrom CT, Oakeshott J, Jørgensen PS, Zalucki MP, et al. 2011. Evolutionary principles and their practical application. Evol Appl. 4(2):159–183. doi:10.1111/j.1752-4571.2010.00165.x.

Hinde RA. 1976. Interactions, relationships and social structure. Man. 11(1):1–17.

Hirotani A. 1990. Social organization of reindeer (*Rangifer tarandus*), with a special reference to relationships among females. Can J Zool. 68(4):743–749.

Hofmann HA, Beery AK, Blumstein DT, Couzin ID, Earley RL, Hayes LD, Hurd PL, Lacey EA, Phelps SM, Solomon NG, et al. 2014. An evolutionary framework for studying mechanisms of social behavior. Trends Ecol Evol. 29(10):1–9. doi:10.1016/j.tree.2014.07.008.

Huang RKK. 2019. Strategies for sharing space in a predator-prey relationship: drivers for local coyote (*Canis latrans*) and caribou (*Rangifer tarandus*). Memorial University of Newfoundland.

James ARC, Boutin S, Hebert DM, Rippin AB. 2004. Spatial Separation of Caribou From Moose and Its Relation To Predation By Wolves. J Wildl Manage. 68(4):799–809. doi:10.2193/0022-541x(2004)068[0799:ssocfm]2.0.co;2.

Johnson CA, Sutherland GD, Neave E, Leblond M, Kirby P, Superbie C, McLoughlin PD. 2020. Science to inform policy: Linking population dynamics to habitat for a threatened species in Canada. J Appl Ecol. 57(7):1314–1327. doi:10.1111/1365-2664.13637.

Joly K, Chapin FS, Klein DR. 2010. Winter habitat selection by caribou in relation to lichen abundance, wildfires, grazing, and landscape characteristics in northwest Alaska. Écoscience. 17(3):321–333. doi:10.2980/17-3-3337.

Jung TS, Larter NC, Allaire DG. 2019. Social organization of boreal woodland caribou (*Rangifer tarandus caribou*) in response to decreasing annual snow depth. Mammal ReLsearch. 64(3):377–385.

Kappeler PM, Barrett L, Blumstein DT, Clutton-Brock TH. 2013. Constraints and flexibility in mammalian social behaviour: introduction and synthesis. Philos Trans R Soc. 368(1618):20120337. doi:10.1098/rstb.2012.0337.

Kinnison MT, Hairston NG. 2007. Eco-evolutionary conservation biology: Contemporary evolution and the dynamics of persistence. Funct Ecol. 21(3):444–454. doi:10.1111/j.1365-2435.2007.01278.x.

Krause J, Lusseau D, James R. 2009. Animal social networks: An introduction. Behav Ecol Sociobiol. 63(7):967–973. doi:10.1007/s00265-009-0747-0.

Lafontaine A, Drapeau P, Fortin D, Gauthier S, Boulanger Y, St-Laurent M. 2019. Exposure to historical burn rates shapes the response of boreal caribou to timber harvesting. Ecosphere. 10(5):e02739. doi:10.1002/ecs2.2739.

Laskowski KL, Modlmeier AP, DeMarco AE, Coleman A, Zhao K, Brittingham HA, McDermott DR, Pruitt JN. 2014. Retraction: Persistent social interactions beget more pronounced personalities in a desert-dwelling social spider. Biol Lett. 10(8):20200062. doi:10.1098/rsbl.2014.0419.

Laskowski KL, Montiglio P-O, Pruitt JN. 2020. Retraction: "Individual and group performance suffers from social niche disruption." Am Nat. 195(2):393. doi:10.1086/708066.

Laskowski KL, Pruitt JN. 2014. Retraction: Evidence of social niche construction: Persistent and repeated social interactions generate stronger personalities in a social spider. Proc R Soc B Biol Sci. 281(1783):2020. doi:10.1098/rspb.2013.3166.

Leclerc M, Dussault C, St-Laurent MH. 2014. Behavioural strategies towards human disturbances explain individual performance in woodland caribou. Oecologia. 176(1):297–306. doi:10.1007/s00442-014-3012-9.

Lesmerises F, Johnson CJ, St-Laurent M-H. 2018. Landscape knowledge is an important driver of the fission dynamics of an alpine ungulate. Anim Behav. 140:39–47. doi:10.1016/j.anbehav.2018.03.014.

Lewis KP, Mahoney SP. 2014. Caribou survival, fate, and cause of mortality in Newfoundland: a summary and analysis of the patterns and causes of caribou survival and mortality in Newfoundland during a period of rapid population decline (2003-2012). Tech Bull No 009, Sustain Dev Strateg Sci Gov Newfoundl Labrador, St John's, NL.

Losier CL, Couturier S, St-Laurent MH, Drapeau P, Dussault C, Rudolph T, Brodeur V, Merkle JA, Fortin D. 2015. Adjustments in habitat selection to changing availability induce fitness costs for a threatened ungulate. J Appl Ecol. 52(2):496–504. doi:10.1111/1365-2664.12400.

Madliger CL, Cooke SJ, Crespi EJ, Funk JL, Hultine KR, Hunt KE, Rohr JR, Sinclair BJ, Suski CD, Willis CKR, et al. 2016. Success stories and emerging themes in conservation physiology. Conserv Physiol. 4(November 2015):1–17. doi:10.1093/conphys/cov057.

Mahoney SP, Lewis KP, Weir JN, Morrison SF, Luther GJ, Schaefer JA, Pouliot D, Latifovic R. 2016. Woodland caribou calf mortality in Newfoundland: insights into the role of climate, predation and population density over three decades of study. Popul Ecol. 58(1):91–103. doi:10.1007/s10144-015-0525-y.

Mahoney S.P., Schaefer JA. 2002. Long-term changes in demography and migration of Newfoundland caribou. J Mammal. 83(4):957–963.

Mahoney Shane P., Schaefer JA. 2002. Hydroelectric development and the disruption of migration in caribou. Biol Conserv. 107(2):147–153. doi:10.1016/S0006-3207(02)00052-6.

Mahoney SP, Virgl JA. 2003. Habitat selection and demography of a nonmigratory woodland caribou population in Newfoundland. Can J Zool. 81(2):321–334. doi:10.1139/z02-239.

Mahoney SP, Weir JN, Luther JG, Schaefer JA, Morrison SF. 2011. Morphological change in Newfoundland caribou: Effects of abundance and climate. Rangifer. 31(1):21–34. doi:10.7557/2.31.1.1917.

Makagon MM, McCowan B, Mench JA. 2012. How can social network analysis contribute to social behavior research in applied ethology? Appl Anim Behav Sci. 138:152–161. doi:10.1016/j.applanim.2012.02.003.

Mallory CD, Boyce MS. 2017. Observed and predicted effects of climate change on Arctic caribou and reindeer. Environ Rev. 13(June):1–13.

Mayor SJ, Schaefer JA, Schneider DC, Mahoney SP. 2009. The spatial structure of habitat selection: A caribou's-eye-view. Acta Oecologica. 35(2):253–260. doi:10.1016/j.actao.2008.11.004.

McCue AJ, McGrath MJ, Wiersma YF. 2014. Benefits and drawbacks of two modelling approaches for a generalist carnivore: can models predict where Wile E. Coyote will turn up next? Int J Geogr Inf Sci. 28(8):1590–1609. doi:10.1080/13658816.2013.847444.

McGrath D. 2004. The Newfoundland Coyote. 1st ed. St. John's, Newfoundland: DRC Publishing.

McLaren BE, Mahoney SP, Porter TS, Oosenbrug SM. 2000. Spatial and temporal patterns of use by moose of pre-commercially thinned, naturally-regenerating stands of balsam fir in central Newfoundland. For Ecol Manage. 133(3):179–196. doi:10.1016/S0378-1127(99)00223-6.

McLaren BE, Roberts BA, Djan-Chekar N, Lewis KP. 2004. Effects of overabundant moose on the Newfoundland landscape. Alces. 40(February 2015):45–59.

Morris DW. 2003. Toward an ecological synthesis: a case for habitat selection. Oecologia. 136(1):1–13. doi:10.1007/s00442-003-1241-4.

Mumma MA, Soulliere CE, Mahoney SP, Waits LP. 2014. Enhanced understanding of predator-prey relationships using molecular methods to identify predator species, individual and sex. Mol Ecol Resour. 14(1):100–108. doi:10.1111/1755-0998.12153.

Nicolaus M, Tinbergen JM, Ubels R, Both C, Dingemanse NJ. 2016. Density fluctuations

represent a key process maintaining personality variation in a wild passerine bird. Ecol Lett. 19:478–486. doi:10.1111/ele.12584.

O'Brien PP, Webber QMR, Vander Wal E. 2018. Consistent individual differences and population plasticity in network-derived sociality: An experimental manipulation of density in a gregarious ungulate. PLoS One. 13(3):e0193425.

Peignier M, Webber QMR, Koen EL, Laforge MP, Robitaille AL, Vander Wal E. 2019. Space use and social association in a gregarious ungulate: Testing the conspecific attraction and resource dispersion hypotheses. Ecol Evol. 9:5133–5145. doi:10.1002/ece3.5071.

Pelletier F, Clutton-Brock T, Pemberton J, Tuljapurkar S, Coulson T. 2007. The evolutionary demography of ecological change: Linking trait variation and population growth. Science (80-). 315(5818):1571–1574. doi:10.1126/science.1139024.

Prichard AK, Parrett LS, Lenart EA, Caikoski JR, Joly K, Person BT. 2020. Interchange and Overlap Among Four Adjacent Arctic Caribou Herds. J Wildl Manage.:1–15. doi:10.1002/jwmg.21934.

Pruitt JN, Bolnick DI, Sih A, DiRienzo N, Pinter-Wollman N. 2016. Authorship removal correction for "Behavioural hypervolumes of spider communities predict community performance and disbandment." Proc R Soc B Biol Sci. 283(1844):2020. doi:10.1098/rspb.2016.1409.

Pruitt JN, Howell KA, Gladney SJ, Yang Y, Lichtenstein JLL, Spicer ME, Echeverri SA, Pinter-Wollman N. 2017. Behavioral hypervolumes of predator groups and predator-predator interactions shape prey survival rates and selection on prey behavior. Am Nat. 189(3):254–266. doi:10.1086/690292.

Pruitt Jr. WO. 1959. Snow as a factor in the winter ecology of the barren ground caribou (*Rangifer arcticus*). Arctic. 12(3):158–179.

Robitaille AL, Webber QMR, Vander Wal E. 2019. Conducting social network analysis with animal telemetry data: applications and methods using spatsoc. Methods Ecol Evol. 10:1203–1211. doi:10.1111/2041-210X.13215.

Rose P, Croft D. 2015. The potential of Social Network Analysis as a tool for the management of zoo animals. Anim Welf. 24(2):123–138. doi:10.7120/09627286.24.2.123.

Rushmore J, Caillaud D, Matamba L, Stumpf RM, Borgatti SP, Altizer S. 2013. Social network analysis of wild chimpanzees provides insights for predicting infectious disease risk. J Anim Ecol. 82(5):976–986. doi:10.1111/1365-2656.12088.

Schaefer JA, Mahoney SP. 2007. Effects of Progressive Clearcut Logging on

Newfoundland Caribou. J Wildl Manage. 71(6):1753–1757. doi:10.2193/2005-479.

Schaefer JA, Mahoney SP. 2013. Spatial dynamics of the rise and fall of caribou (*Rangifer tarandus*) in Newfoundland. Can J Zool. 91(11):767–774. doi:10.1139/cjz-2013-0132.

Schaefer JA, Mahoney SP, Weir JN, Luther JG, Soulliere CE. 2016. Decades of habitat use reveal food limitation of Newfoundland caribou. J Mammal. 97(2):386–393. doi:10.1093/jmammal/gyv184.

Serrouya R, Seip DR, Hervieux D, McLellan BN, McNay RS, Steenweg R, Heard DC, Hebblewhite M, Gillingham M, Boutin S. 2019. Saving endangered species using adaptive management. Proc Natl Acad Sci.(27):1–6. doi:10.1073/pnas.1816923116.

Silk MJ, Croft DP, Delahay RJ, Hodgson DJ, Boots M, Weber N, McDonald RA. 2017. Using social network measures in wildlife disease ecology, epidemiology, and management. Bioscience. 67(3):245–257. doi:10.1093/biosci/biw175.

Smith KF, Acevedo-Whitehouse K, Pedersen a. B. 2009. The role of infectious diseases in biological conservation. Anim Conserv. 12(1):1–12. doi:10.1111/j.1469-1795.2008.00228.x.

Spiegel O, Leu ST, Sih A, Bull CM. 2016. Socially interacting or indifferent neighbours? Randomization of movement paths to tease apart social preference and spatial constraints. Methods Ecol Evol. 7:971–979. doi:10.1111/2041-210X.12553.

Stanton MA, Mann J. 2012. Early Social Networks Predict Survival in Wild Bottlenose Dolphins. PLoS One. 7(10):1–6. doi:10.1371/journal.pone.0047508.

Sutherland WJ. 1998. The importance of behavioural studies in conservation biology. Anim Behav. 56(4):801–809. doi:10.1006/anbe.1998.0896.

Tregenza T. 1995. Building on the Ideal Free Distribution. Adv Ecol Res. 26(C):253–307. doi:10.1016/S0065-2504(08)60067-7.

Vors LS, Boyce MS. 2009. Global declines of caribou and reindeer. Glob Chang Biol. 15(11):2626–2633. doi:10.1111/j.1365-2486.2009.01974.x.

Vors LS, Schaefer JA, Pond BA, Rodgers AR, Patterson BR. 2007. Woodland caribou extirpation and anthropogenic Landscape Disturbance in Ontario. J Wildl Manage. 71(4):1249–1256. doi:10.2193/2006-263.

Vander Wal E, Festa-Bianchet M, Réale D, Coltman DW, Pelletier F. 2015. Sex-based differences in the adaptive value of social behavior contrasted against morphology and environment. Ecology. 96(3):631–641. doi:10.1890/14-1320.1.sm.

Vander Wal E, Webber QMR. 2020. Density dependence and eco-evolutionary dynamics of animal social networks: a comment on Shizuka and Johnson. Behav Ecol. 31:16–18. doi:10.1093/beheco/arz150.

Webber QMR, Brigham RM, Park AD, Gillam EH, O'Shea TJ, Willis CKR. 2016. Social network characteristics and predicted pathogen transmission in summer colonies of female big brown bats (*Eptesicus fuscus*). Behav Ecol Sociobiol. 70(5):701–712. doi:10.1007/s00265-016-2093-3.

Webber QMR, Vander Wal E. 2018. An evolutionary framework outlining the integration of individual social and spatial ecology. J Anim Ecol. 87(1):113–127. doi:10.1111/1365-2656.12773.

Webber QMR, Vander Wal E. 2019. Trends and perspectives on the use of animal social network analysis in behavioural ecology: a bibliometric approach. Anim Behav. 149:77–87. doi:10.1016/j.anbehav.2019.01.010.

Webber QMR, Vander Wal E. 2020. Heterogeneity in social network connections is density-dependent: implications for disease dynamics in a gregarious ungulate. Behav Ecol Sociobiol. 74(77):1–13.

Weir JN, Mahoney SP, McLaren B, Ferguson SH. 2007. Effects of Mine Development on Woodland Caribou Rangifer Tarandus Distribution. Wildlife Biol. 13(1):66–74. doi:10.2981/0909-6396(2007)13[66:eomdow]2.0.co;2.

Weir JN, Morrison SF, Luther JG, Mahoney SP. 2014. Status of the Newfoundland population of woodland caribou.

Wey T, Blumstein DT, Shen W, Jordán F. 2008. Social network analysis of animal behaviour: a promising tool for the study of sociality. Anim Behav. 75(2):333–344. doi:10.1016/j.anbehav.2007.06.020.

Whitehead H. 2008. Analyzing animal societies: quantitative methods for vertebrate social analysis. University of Chicago Press.

Williams R, Lusseau D. 2006. A killer whale social network is vulnerable to targeted removals. Biol Lett. 2(May):497–500. doi:10.1098/rsbl.2006.0510.

Wilson ADM, Krause S, Dingemanse NJ, Krause J. 2013. Network position: A key component in the characterization of social personality types. Behav Ecol Sociobiol. 67(1):163–173. doi:10.1007/s00265-012-1428-y.

Witter LA, Johnson CJ, Croft B, Gunn A, Gillingham MP. 2012. Behavioural trade-offs in response to external stimuli: Time allocation of an Arctic ungulate during varying intensities of harassment by parasitic flies. J Anim Ecol. 81(1):284–295. doi:10.1111/j.1365-2656.2011.01905.x.

Wittmer HU, McLellan BN, Seip DR, Young JA, Kinley TA, Watts GS, Hamilton D. 2005. Population dynamics of the endangered mountain ecotype of woodland caribou (Rangifer tarandus caribou) in British Columbia, Canada. Can J Zool. 83(3):407–418. doi:10.1139/z05-034.

Wolf JB, Brodie EBI, Cheverud JM, Moore AJ, Wade MJ. 1998. Evolutionary consequences of indirect genetic effects. Science (80-). 13(2):64–69.

CHAPTER 2:AN EVOLUTIONARY FRAMEWORK OUTLINING THE INTEGRATION OF INDIVIDUAL SOCIAL AND SPATIAL ECOLOGY

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2.1 Summary

1. Behaviour is the interface between an organism and its environment, and behavioural plasticity is important for organisms to cope with environmental change. Social behaviour is particularly important because sociality is a dynamic process, where environmental variation influences group dynamics and social plasticity can mediate resource acquisition. Heterogeneity in the ecological environment can therefore influence the social environment. The combination of the ecological and social environments may be interpreted collectively as the 'socioecological' environment', which could explain variation in fitness.

2. My objective was to outline a framework through which individual social and spatial phenotypes can be integrated and interpreted as phenotypes that covary as a function of changes in the socioecological environment. I propose the socioecological environment is composed of individual behavioural traits, including sociality and habitat selection, both of which are repeatable, potentially heritable, and may reflect animal personality traits. I also highlight how ecological and social niche theory can be applied to the socioecological environment framework, where individuals occupy different socioecological niches. Individual sociality and habitat selection are also density-dependent, and theory predicts that density-dependent traits should affect reproduction, survival, and therefore fitness and population dynamics.

3. I then illustrate the proximate links between sociality, habitat selection, and fitness as well as the ultimate, and possibly adaptive, consequences associated with changes in population density. The ecological, evolutionary, and applied implications of my proposed socioecological environment framework are broad and changes in density could

influence individual fitness and population dynamics. For instance, human induced environmental changes can influence population density, which can affect the distribution of social and spatial phenotypes within a population. In summary, I outline a conceptual framework that incorporates individual social and spatial behavioural traits with fitness and I highlight a range of ecological and evolutionary processes that are likely associated with the socioecological environment.

2.2 Introduction

Sociality is common among animals and is a continuum on which species and individuals exist (Alexander, 1974). Sociality broadly refers to interactions among conspecifics in which individuals can display social plasticity, while populations or species can adapt socially; both of which are critical for dealing with environmental change (Hofmann *et al.* 2014). Individual sociality and the social structures in which individuals exist are highly variable and decisions about sociality are optimized to maximize individual fitness (Silk 2007; Farine, Montiglio & Spiegel 2015). Although links between sociality and fitness are becoming increasingly established (Silk 2007), this relationship may vary spatiotemporally (Naud et al., 2016). For instance, predation risk and resource availability vary depending on an individual's social position, a relationship which can change through time and space (Hirsch 2007). As biophysical environmental conditions change spatiotemporally, it becomes important to understand individual variation in resource selection and sociality, and how these traits combine to influence fitness.

Environmental heterogeneity affects social and spatial behaviours, such as social centrality and habitat selection (see definitions below), where spatial and temporal heterogeneity in resources can generate social conflict leading to alternative decisions on resource selection (Sueur *et al.* 2011). Individual differences in social centrality, defined as '*the extent to which an individual is connected to other individuals*' (Brent, 2015), and social conflict can affect the relationship between sociality and fitness. Specifically, fission-fusion dynamics are one form of social conflict leading to temporary spatial segregation, which can be adaptive (e.g., Haydon *et al.* 2008) or maladaptive (e.g.,

Sigaud *et al.* 2017). Individuals are expected to benefit from fission-fusion by reduced competition during foraging, a process which could occur through social familiarity. For example, spotted hyaenas (*Crocuta crocuta*) adjusted grouping behaviour through fission-fusion in response to changes in feeding competition (Smith *et al.* 2008), while in great tits (*Parus major*), fledging success was greater for females with socially familiar neighbours (Grabowska-Zhang, Wilkin & Sheldon 2011). These examples highlight how fission-fusion dynamics are a product of ecological variation, but also the catalyst for producing a social environment that can affect fitness. The social environment reflects interactions among conspecifics that occur during a specific time-frame (Saltz, Geiger, Anderson, Johnson, & Marren, 2016), and fission-fusion may represent a possible link between social and ecological environments.

A promising route linking fission-fusion and fitness exists through understanding how individuals interact with their environment through habitat selection (Morris 2011) and through social attraction (Fletcher, 2009). I adopt the definition of habitat used by Morris (2003), where habitat is: '*a spatially-bounded area, with a subset of physical and biotic conditions, within which the density of interacting individuals, and at least one of the parameters of population growth, is different than in adjacent subsets*'. While this definition of habitat is idealistic, it is important to note that natural systems are often difficult to delineate as stringently. Habitat selection determines the spatiotemporal distribution of individuals with consequences for individual behaviour, population dynamics, and intra-specific interactions (Morris 2011; van Beest *et al.* 2014). Theoretically, individuals select habitat that maximizes fitness (McLoughlin *et al.* 2010), illustrating the adaptive value of habitat selection. Heterogeneity in the spatiotemporal

distribution of resources reveals strategies of resource selection, where individuals can range from resource specialists to generalists, a process that indicates that resources are selected along a gradient (Fortin, Morris & McLoughlin 2008). Resource gradients reflect heterogeneous environments, which favour fission-fusion dynamics (Sueur *et al.* 2011). Therefore, variation in habitat selection as a function of spatiotemporal variation in resources, could affect social interactions among individuals (Fortin et al., 2009; Haydon et al., 2008), individual fitness and, in turn, population dynamics.

Environmental heterogeneity promotes population-level variation in individual behaviour because different phenotypes have different adaptive values through space and time. Although individual social and spatial behaviour are important, social and ecological environments are particularly likely to covary. The social environment can therefore be perceived as a reflection of the ecological environment and the combined 'socioecological' environment represents a novel intersection between individual sociality and habitat selection, which could explain variation in fitness. Intra-specific variation in habitat selection and sociality are therefore inherently linked through the socioecological environment (Figure 2.1). Adaptive (co)variation in the relationship between habitat selection and sociality could also be subject to selection as individuals maximize fitness. Individual social and ecological environments are highly dynamic, e.g., through fission-fusion, and individuals likely differ in their responses to environmental (social and ecological) heterogeneity. Individual variation is therefore the crux of the socioecological environment and reflects the phenotypes upon which natural selection acts.

To fully elucidate the relationships between sociality, habitat selection, and fitness, I have four objectives:

1. We interpret components of the socioecological environment as animal personality or behavioural syndromes. I then propose that traits associated with the socioecological environment are density-dependent and can affect population dynamics (Figure 2.1).

2. We apply niche theory to the socioecological environment and discuss possible implications of individual fitness in the context of ecological and social niche theory. I also address individual niche specialization and suggest that social and ecological niches likely covary and are repeatable across time or contexts and could therefore reflect an axis of animal personality in the context of the socioecological environment.

3. We propose two conceptual models informed by behavioural ecology and habitat selection theory. These models are thought experiments that include: 1) an illustration of an adaptive landscape used to quantify density-dependent changes in the socioecological environment (Box 1); and 2) a hypothetical fission-fusion society where density-dependent habitat selection and sociality covary to affect fitness (Box 2).

4. We conclude by summarizing my synthesis of the socioecological environment and generalize my conceptual framework by discussing possible ecological, evolutionary, and applied implications. I also propose four testable hypotheses, with associated predictions, which could be tested under the framework I develop here (Table 2.1). I avoid developing my narrative with a specific system in mind so the framework can serve as a general tool for researchers to generate predictions, test hypotheses, and apply it broadly to specific systems (but see Table 2.3 for examples).

2.3 Implications of density-dependent behaviours on population ecology

In the context of the socioecological environment, the link between individual behavioural traits and population ecology may exist through an eco-evolutionary feedback between the distribution of behavioural phenotypes and population dynamics (Figure 2.1; Ezard, Côté & Pelletier 2009). This feedback is possible when environmental conditions affect population density, therefore altering the adaptive value of the trait, which in turn influences the population-level distribution of individual-based phenotypes (Figure 2.1). The feedback is completed if the phenotype(s) affect population ecology parameters, such as survival and reproduction, which inherently affect population density (Figure 2.1).

Density dependence is important for the socioecological environment because changes in density are linked to changing fitness proxies. Our understanding of density dependence can help predict how behavioural mechanisms associated with habitat selection influence parameters of population growth (Morris 2011). Density dependence transcends scales, where the ecological perspective is similar between local and population densities, but the mechanism differs. Density-dependent habitat selection is predicated on the assumption of limited availability of resources per individual at the population scale, but access to resources at the local scale. Habitat selection is density-dependent and has received significant theoretical and empirical attention (Morris 2003; Fortin, Morris & McLoughlin 2008; van Beest *et al.* 2014). An increase in local density via social aggregation can decrease the per capita risk of predation, but predator success may increase as a function of density (Pettorelli *et al.* 2011). However, conspecific competition for resources also changes with overall population density (Hansen *et al.*

1999) and social behaviours, such as interaction duration or rate, are often density-dependent (Brashares, Werner, & Sinclair, 2010; Vander Wal, Yip, & McLoughlin, 2012).

Individual components of the socioecological environment, including social behaviour and habitat selection, could be interpreted as animal personality, i.e., consistent individual differences in behaviour (Sih, Bell, Johnson, & Ziemba, 2004). The integration of sociality, habitat selection, and animal personality represents an important advance in behavioural ecological theory (for examples integrating sociality and personality see Krause, James & Croft 2010; Wilson *et al.* 2013). The socioecological environment is not itself a measurable trait, but rather it is the combination of social and ecological factors that drive (co)variation between individual social and spatial phenotypes. If these traits are repeatable and correlated, they could be interpreted individually as animal personality. Repeatability (r) is a critical aspect of animal personality and is quantified as:

$$r = \frac{V_{among}}{V_{among} + V_{within}} \; [Equation\ 1]$$

where V_{among} is among-individual variation and V_{within} is within-individual variation (Bell, Hankison & Laskowski 2009). Individually repeatable traits associated with the socioecological environment, such as social centrality (Aplin et al., 2015; Vander Wal, Festa-Bianchet, Réale, Coltman, & Pelletier, 2015) and habitat selection (Leclerc et al., 2016), could be interpreted as a socioecological behavioural syndrome, i.e., a suite of personality traits that are correlated across time and contexts (Sih, Cote, Evans, Fogarty, & Pruitt, 2012). Traits which comprise behavioural syndromes are also repeatable and these correlations are likely driven by underlying genetic covariation. The relationship between social and spatial behavioural traits and fitness is important because consistent

correlations among behaviours across changes in population density could represent a potential adaptive landscape, where fitness varies as a function of the correlation between social and spatial traits (for detailed illustration see Box 1). Although animal personality is focused broadly within evolutionary and behavioural ecology, and personality can be quantified relatively easily, it is through theoretical and practical approaches that I aim to ground my integration of personality within the socioecological environment.

The animal personality concept purports that individual behaviours are consistent across time and context and are likely the result of adaptive evolution (Wolf & Weissing 2010). However, plasticity is an important aspect of behavioural variation because it allows individuals within a population to respond appropriately to environmental variation and optimize fitness (DeWitt, Sih & Wilson 1998). Behaviour is not infinitely plastic and individuals are often limited in their responses through constraints in sensory processing, cognitive ability, and morphology (Mathot & Dingemanse, 2015). While personality traits were historically interpreted as consistent, and thus relatively fixed, an exciting aspect of personality research incorporates behavioural plasticity associated with personality traits (Brommer, 2013). Specifically, personality incorporates aspects of plasticity and individuals should respond appropriately, but consistently relative to conspecifics, to changing environments (e.g., using behavioural reaction norms: Mathot *et al.* 2012). Moreover, repeatability of behavioural plasticity, for instance year-to-year repeatability, is adaptive when costs associated with plasticity decrease with an individual's experience to environmental variation (Wolf, van Doorn, & Weissing, 2008). Indeed, while behavioural plasticity can be adaptive, personality explains a large proportion of variation in behavioural plasticity (Nussey, Wilson & Brommer 2007;

Dingemanse *et al.* 2010) and the integration of animal personality and quantitative genetics has confirmed the importance of genetic and environmental effects in personality-related differences in plasticity (Dochtermann, Schwab, & Sih, 2015; Mathot & Dingemanse, 2015).

The application of quantitative genetics in the context of the socioecological environment could elucidate underlying genetic mechanisms which drive variation in social and spatial phenotypes. Selection can have direct and indirect genetic effects (DGEs and IGEs, respectively), where DGEs are the effect of an individual's own genotype on their phenotype and IGEs are the effect of a conspecifics genotype on the focal individual's phenotype (Bijma & Wade, 2008; Ellen et al., 2016). IGEs may be important for the evolution of social behaviour because social plasticity could arise as a function of phenotypes expressed by conspecifics (Dingemanse & Araya-Ajoy 2015), a process which could be particularly important for our understanding of the socioecological environment. If habitat selection is linked to social cues from conspecifics (Fletcher 2007), IGEs could also be important for understanding how individuals rely on conspecifics for information about habitat quality. In the context of the socioecological environment, IGEs can be proximately manifested as inter-individual interactions, such as aggression (Wilson, Gelin, Perron, & Réale, 2009), or emergent properties of a social group, such as group phenotypic composition (Farine et al., 2015), and these processes can ultimately explain variance in individual behaviours as well as the population-level distribution of a given behaviour.

Changing population density has potential as a selective pressure which can alter the socioecological environment. At high population density one might expect an

increase in competition for resources, which could affect social aggregation and spatial distribution of individuals (Box 2). Changes in population density, or other environmental variables, can influence the relationship between social or spatial behaviours and fitness, and represent a gradient across which fitness is maximized (Sih 2013). A given social or spatial behaviour is adapted to the environment in which the genotype controlling the phenotype reproduces at least once, and to be adaptive these behavioural phenotypes must vary at the population-level across an environmental gradient (i.e., with minima, maxima, and a mean). In the case of the socioecological environment, individuals range along a social continuum from highly social to relatively asocial (Wey *et al.* 2008) and a habitat selection continuum from specialist to generalist (Fortin, Morris & McLoughlin 2008). If environment conditions associated with a behavioural phenotype change, there could be a mismatch between the original distribution of phenotypes, which matched the historical environment, and the current environment (Hendry *et al.* 2011). The distinction of individually-based traits with a given population-level distribution is important because a hypothetical repeatable and heritable behavioural phenotype may be well-suited to the historical environment, but is maladaptive in the current environment. While individual plasticity is typically sufficient to cope with most environmental perturbations, behavioural adaptation occurs when a subset of individuals reproduce and another subset of individuals fail to reproduce.

Maladaptive phenotypes result in reduced reproduction and survival, which subsequently change population density and can result in a shift in the adaptive capacity of a given phenotypic trait. Behavioural plasticity is important because, in the context of the socioecological environment, maladaptive behavioural responses can affect how

animals forage or disseminate social information about novel food patches. For instance, bison (*Bison bison*) are hunted at higher rates on agricultural patches, but bison that foraged on agricultural patches for the first time were more likely to access these patches with bison that had previously foraged on these patches (Sigaud et al., 2017). Although using agricultural patches may provide proximal benefits, i.e., higher quality or quantity of forage, ultimately, this behaviour is maladaptive because it reduces survival. As population density changes, behavioural plasticity could improve an animal's ability to use social or spatial cues to access resources. This type of behavioural response could shape future evolution and facilitate a phenotypic transition from one adaptive peak to another (Sih, Ferrari & Harris 2011). Moreover, while natural fluctuations in density are common, anthropogenic factors can expedite changes in density (negatively or positively) and alter the distribution of density-dependent phenotypic traits in the population.

As individually quantifiable components of the socioecological environment, sociality and habitat selection are linked through possible (co)variation in response to changes in population density. Density is a selective agent for habitat selection and some social behaviours and could be incorporated into a feedback loop (Figure 2.1). Few studies have empirically quantified the relationship between sociality, habitat selection, and population density. In an experimental manipulation, flycatchers (*Empidonax minimus*) and American redstarts (*Setophaga ruticilla*) used social cues about habitat settlement, a process which was strongest at moderate densities (Fletcher 2007). Social cues may also be related to site fidelity, such that individuals that settle in the same area may have stronger social relationships and therefore greater trust in the social cues being exchanged. At low densities, individual birds received little benefit from social cues,

while at high densities, competition was costly and individuals did not display social cues (Fletcher 2007). Meanwhile, vigilance behaviour and territorial vocalizations, i.e., aspects of social behaviour, were higher for red squirrels (*Tamiasciurus hudsonicus*) at food-supplemented sites where squirrel density was consistently high (Dantzer *et al.* 2012). While these examples represent valuable contributions linking sociality, habitat selection, and density, density-dependent changes in the trait distribution of adaptive social and spatial phenotypes could affect reproduction, survival, and ultimately fitness.

2.4 The Application of Niche Theory

2.4.1 Ecological Niche

The socioecological environment can also be integrated with other ecological concepts. An ecological niche is a species distribution that is constrained based on the '*biophysical and environmental conditions across geographical space*' (Soberón 2007; Trainor & Schmitz 2014). Ecological niches are quantified using species distribution models (SDMs), by denoting the area occupied by a species, compared to the available area, as a function of a set of environmental variables which constrain or facilitate species persistence (Trainor & Schmitz 2014). Within a species distribution and ecological niche, fitness varies because resources and competitors are heterogeneous, resulting in a series of optimal biophysical and ecological conditions where fitness is optimized (Trainor & Schmitz 2014). Fitness can be visualized using contours that represent biophysical space (i.e., niches) with equal fitness levels as contours (Soberón 2007). Inherently, a model with fitness contours also assumes intra-specific variation (or "internal structure", *sensu* Trainor & Schmitz 2014), indicating that individuals possess a range of phenotypic characteristics (e.g., behavioural, physiological, or life-history traits) which allows them

to optimize fitness based on spatiotemporal variation in resources within their biophysical environment. This process is equivalent to the adaptive landscape concept (Box 1), where individuals occupy social and ecological environments that maximize fitness.

Differences in habitat selection among individuals within a population has been interpreted as an 'individual niche' (Bolnick *et al.* 2003), where an ecological environment is partitioned among individuals and occupied differentially. Ecologically, the niche concept could help explain intra-specific variation in behavioural processes, such as diet specialization (Araújo, Bolnick & Layman 2011), while evolutionarily, these behavioural processes could explain variation in fitness. The fundamental assumptions underlying niche theory can be transferred to the classic habitat selection literature (Morris 2003). Fine-grained habitat selection is often quantified with resource selection analyses (e.g., step selection functions: Fortin *et al.* 2005; ecological niche factor analysis: Basille *et al.* 2008; resource selection functions: McLoughlin *et al.* 2010; integrated step selection functions: Avgar *et al.* 2016). Resource selection functions (RSFs) are likely the most commonly used method and are defined by characteristics measured on resource units such that selection of a unit is modelled as being proportional to the probability of a unit being occupied by an individual (Manly *et al.* 2002; McLoughlin *et al.* 2010). Similar to SDMs, RSFs represent spatiotemporal selection of resources by an individual, or population, relative to randomly distributed available habitat and can reflect habitat selection for an individual or population-level subset of the SDM. The sum of all individual RSFs are equal to the SDM and emerging theoretical and empirical evidence suggests individual behavioural consistency in resource selection (Leclerc *et al.* 2016; Matthiopoulos *et al.* 2015).

At the intra-specific level, individuals make resource selection decisions to maximize fitness. For example, in female red deer (*Cervus elaphus*) lifetime reproductive success (LRS) was higher for grassland specialists at low densities, whereas habitat generalists had higher LRS at high densities (McLoughlin *et al.* 2006). An individual's RSF, i.e., ecological niche, can be considered along a gradient, ranging from resource specialists to generalists, a process which is density-dependent (Fortin, Morris & McLouglin 2008). Moreover, habitat selection can influence fitness (e.g., adult reproductive success: McLoughlin *et al.* 2006; survival: DeCesare *et al.* 2014), suggesting that, if repeatable and heritable, variation in habitat selection is evolutionarily adaptive (Wolf & Weissing 2010). For example, brown bears (*Ursus arctos*) selected for bogs and timber-harvest cut blocks, and this behaviour was strongly repeatable over time, providing empirical evidence for consistent individual differences in habitat selection (Leclerc *et al.* 2016). Animal personality theory could therefore contribute to the habitat selection and individual niche concepts and is one possible mechanism explaining individual variation in habitat and resource selection.

2.4.2 Social Niche

Niche theory can also be readily applied to social specialization, where the social environment is analogous to the ecological environment and individuals occupy specific social niches (Montiglio, Ferrari, & Réale, 2013). This integration is highly relevant to the socioecological environment. While consensus to adequately define a 'social niche' is lacking, I rely on the definition proposed by Saltz *et al.* (2016), where '*the social niche is the set of social environments in which the focal individual has non-zero inclusive fitness*'. Importantly, this definition incorporates fitness which, based on ecological niche

theory, should be optimized as a function of the social environment and individual behaviour to generate social niches (Saltz *et al.* 2016). The inclusion of fitness also provides an important analogue to Morris's (2003) definition of habitat, where fitness is affected by variation in a phenotypic trait (social or spatial) across environments that differ in at least one parameter of population growth (e.g., survival or reproduction). This parallel is important in the context of the socioecological environment because I expect social and spatial phenotypes to differentially affect fitness as a function of density (Box 1), an expectation which extends to individual-based social and ecological niche theory. Moreover, the analogy between ecological and social niches also relies on fitness, and, by co-opting ecological niche theory, an individual's social niche could be mapped using fitness contours, e.g., an adaptive landscape (Box 1), to denote variation in fitness across social and ecological environments.

Similar to an individual ecological niche (Bolnick *et al.* 2003), social niche specialization also assumes consistent individual differences in behaviour. Individual differences in social niches should arise when different social environments favour different behavioural phenotypes (Saltz *et al.* 2016). Individual differences in social associations can emerge from the population-wide social niche, and between-individual variation in social niche specialization could be adaptive. Social niche specialization could arise through several possible behavioural mechanisms. Stable and predictable behavioural differences among group members along with repeated interactions among individuals could reinforce social specialization and result in the development of social niches (Montiglio, Ferrari & Réale 2013). For example, spider colonies that interacted frequently had similar consistency in social behaviours, indicating colony similarity

could maintain the social niche (Laskowski & Pruitt 2014). Note, Laskowski & Pruitt (2014) has been retracted (Laskowski & Pruitt, 2014). In addition, social niche specialization could arise through social assortment (see Table 2.1), where individuals are predicted to assort according to specific phenotypic similarities or dissimilarities. In the context of social niche specializations, individuals may consistently assort according to particular combinations of their own social phenotype and the social phenotypes of conspecifics (Laskowski, Montiglio & Pruitt 2016). Note, Laskowski, Montiglio, & Pruitt (2016) has been retracted (Laskowski, Montiglio, & Pruitt, 2020).

In contrast to ecological niches, consensus on standardized methods for quantifying social niches is lacking, however, social network analyses represent a promising tool for quantifying individual social niches (Saltz et al., 2016). Quantifying aspects of social niches requires social interaction and fitness data to be collected across a range of social environments. Arguably the simplest way to quantify social niches is to quantify the number of social partners of a focal individual, i.e., degree (see Table S2.1 glossary). Determining the identity and social phenotype of a focal individual's social partners adds a layer of complexity to social niche specialization, while determining the repeatability of dyadic social interactions across social environments provides information about an individual's social fidelity (Modlmeier et al., 2014). Note, Modlmeier et al., (2014) has been retracted (Laskowski et al., 2014). While individual social niches can be quantified using network analyses, individually based traits could also be integrated within the broader socioecological and statistical framework that incorporates aspects of animal personality, resource selection functions, and quantitative genetics.

Niche theory provides an opportunity to integrate indirect genetic effects (IGEs) into the socioecological environment framework. Genetic variance is partitioned into direct genetic effects (DGEs), which is synonymous with V_I (genetic variance explained by the phenotype of a focal individual), and IGEs, which is synonymous with V_S (genetic variance explained by the phenotypes of conspecifics). V_I reflects social specialization of a focal individual and V_S reflects social specialization of conspecifics (Dingemanse & Araya-Ajoy 2015). Incorporating IGEs into niche theory could help explain variation in individual social and ecological niche specialization. In the context of the socioecological environment, social phenotypes of conspecifics could affect both social and spatial phenotypes of focal individuals. Individuals range along specialist-generalist social or ecological niche continua (Saltz et al., 2016). The breadth of a social or ecological niche is the total niche width (*TNW*) of all individuals within the population (Bolnick *et al.* 2003):

$$TNW = BIC + WIC \ [Equation\ 2]$$

where *BIC* and *WIC* are the between- and within-individual components of the niche, respectively. *TNW* measures the size of the average individual's niche (Araújo, Bolnick & Layman 2011). To fully integrate niche theory within the conceptual framework of the socioecological environment, I propose a modification to *Equation 2*. Based on *Equation 1*, repeatability is calculated from V_{within} and V_{among}, and *Equation 2* could be modified to calculate ecological or social niche repeatability, as TNW_r:

$$TNW_r = \frac{BIC}{BIC + WIC} \ [Equation\ 3]$$

where *BIC* is equivalent to V_{among} and *WIC* is equivalent to V_{within}. Thus, TNW_r is analogous to *r* and I suggest that by calculating TNW_r, the niche concept could be

effectively translated to the individual niche, where ecological or social niche repeatability could be calculated across time or contexts. Mathematically, *Equation 3* is a simple form of variance partitioning where individual niche variance is attributed to among (*BIC*) and within (*WIC*) individual components of a niche. This extension also empirically links the socioecological environment and niche theory. For instance, similar to quantifying repeatability of habitat selection (for methodological details see Leclerc *et al.* 2016), individual niches may be repeatable and reflect personality traits, while correlations among social and ecological niches could be one component of a socioecological behavioural syndrome.

Niche theory is a foundational ecological concept and, while it has largely been applied at the population and species levels, empirical and theoretical advances (Bolnick et al., 2003; Pruitt et al., 2017) have expanded niche theory to individuals. For instance, individual behaviour and niche theory have recently been integrated as 'behavioural hypervolumes', which is defined as the multi-dimensional behavioural trait space of an individual or population (see Table S2.1 glossary; Pruitt et al. 2016, 2017). Note, Pruitt et al. (2016) has had an authorship correction (Pruitt, Bolnick, Sih, DiRienzo, & Pinter-Wollman, 2016). Ecological and social niche covariance is expected within a behavioural hypervolume context because certain ecological and social niches may facilitate the realization of niche space for the opposite trait. However, if social or ecological environments change, the evolutionary trajectory of an individual's social or ecological niche could be displaced. In red squirrels and eastern chipmunks (*Tamias striatus*), fluctuation in the abundance of food via seed masting can result in fluctuating selection of personality traits where certain individuals have higher fitness when food resources are

abundant versus scarce (Boon, Réale, & Boutin, 2007; Montiglio, Garant, Bergeron, Messier, & Reale, 2014). In the context of the socioecological environment, group size of bison was greater in meadow habitats compared to forested habitats (Fortin et al., 2009), but if meadow niches are altered, covariance between social and ecological phenotypes may be disrupted and the distribution of these traits may shift (Box 1). This shift could therefore alter the range of social niches within the population. I propose that variation in social and spatial phenotypes could, at least partially, be explained by incorporating niche theory, animal personality, and quantitative genetics within the broader framework of the socioecological environment.

2.5 Discussion

We propose a framework through which the socioecological environment, measured as individual social and spatial phenotypes that affect fitness, can be quantified across population densities (Figure 2.1). In my synthetic review, I suggest parallels between ecological and social niche theory and what I term the socioecological environment, while I also argue the socioecological environment is composed of individual-level traits that can be interpreted as animal personality, but collectively may represent a behavioural syndrome. My conceptual models reflect 1) the socioecological environment as a series of adaptive landscapes which change as a function of density (Box 1), and 2) the importance of density-dependent habitat selection and optimal group size theory for fission-fusion dynamics in the context of the socioecological environment (Box 2).

Individual sociality and habitat selection are often density-dependent, and changes in density could alter the distribution of these traits in ways that could affect fitness and population dynamics (Figure 2.1). The shift from one adaptive landscape to another reflects adaptation in social and spatial phenotypes, a process which could be facilitated by behavioural plasticity. While plasticity is important, individual components of the socioecological environment may reflect repeatable, and possibly heritable, personality traits. Correlations between social and spatial personality traits may also reflect a socioecological behavioural syndrome.

Ecological, Evolutionary, and Applied Implications

Variation in the socioecological environment is ultimately driven by changes to the biophysical environment (Figure 2.1). While changes in environmental conditions, such

as population density, can change the distribution of phenotypes within a population, a range of mechanisms exist which could affect the relationship between social or spatial phenotypes and fitness. For instance, animal social and spatial cognitive processes (see Table S2.1 glossary) could be important mechanisms underlying adaptive behaviours (Seyfarth & Cheney, 2015). Specifically, an individual's ability to access and exploit resources is inherently associated with a range of cognitive strategies, including inherited genetic triggers, memory of past experiences, or direct social cues (Fagan et al., 2013; Spiegel & Crofoot, 2016). Factors associated with cognition can therefore influence the proximate relationship between an organism and their socioecological environment. Cognition is an important aspect of the socioecological eco-evolutionary feedback loop linking individual phenotypes to down-stream fitness outcomes (Figure 2.1).

Social and spatial cognition are inherently linked, and in the context of the socioecological environment, fission-fusion dynamics are highly relevant. Fission-fusion dynamics are cognitively complex because individuals are required to process cues from both social and spatial environments (Aureli *et al.* 2008). Individuals form long-lasting social associations with conspecifics who they may not encounter for extended periods of time, and to maintain social cohesion over time individuals must remember former group members. In bison, fission-fusion operates on a short timescale (21 hours: Merkle, Sigaud & Fortin 2015), while for some birds, fission-fusion occurs on a seasonal, or yearly, timescale (Silk *et al.* 2014). Fission-fusion is also a spatial process, where movement decisions associated with the timing of fission or fusion are driven by environmental variation. Species with fission-fusion societies represent potential model systems to test the 'social phenology hypothesis' (Table 2.1), where, for example, seasonal variation in

resources (e.g., foraging resources) may drive changes in covariance of social and spatial phenotypes, and thus fission-fusion dynamic. Whether an animal's decision to fission or fusion occurs on short or long-term time-scales, animals process complex information acquired from, among other things, ecological and social cues (Box 2; Seyfarth & Cheney 2015; Spiegel & Crofoot 2016).

In an applied context, the conceptual framework of the socioecological environment (Figure 2.1) is fundamental to social animals, but is particularly apt for understanding human-induced rapid environmental change (HIREC). The ability to respond to naturally occurring environmental change is typically within the trait distribution observed in a population, however, HIREC can expedite the mismatch between old phenotypes and new environments (Sih et al., 2011; Vander Wal, Garant, Festa-Bianchet, & Pelletier, 2013). Integrating the socioecological environment within HIREC is important because HIREC is predicated on the density-dependent adaptive value of traits that are often affected by human disturbance: habitat selection and social structure. Habitat loss and fragmentation are important aspects of HIREC (Sih et al., 2011), and fragmentation can influence resource selection decisions and social dynamics. Habitat fragmentation can also alter density through changing diversity, availability, or access to resources (e.g., foraging or breeding sites; Tuomainen & Candolin, 2011), processes which could also affect the social environment. For example, in brushtail possums (*Trichosurus cunninghami*), occupancy rates of tree hollows was low in undisturbed areas where trees were abundant, but in fragmented habitats where tree hollow availability decreased, occupancy rates increased, resulting in larger group sizes (Banks *et al.* 2013). For least flycatchers, variation in selection of habitat patches was

modulated by conspecific attraction and social cues (Fletcher 2009), suggesting the social environment can influence, or be influenced by, habitat selection (see details on conspecific attraction and resource dispersion hypotheses in Table 2.1). These examples highlight how ecological and social environments mirror one another, and how changes in one can affect the other, for example, removal of natural corridors could reduce encounter rates among conspecifics. While other aspects of HIREC influence the socioecological environment, habitat fragmentation is a clear example illustrating how social and ecological environments can be decoupled. HIREC associated habitat fragmentation is one mechanism which directly alters the ecological axis of the socioecological environment, and indirectly alters the social axis.

HIREC can cause rapid and persistent declines for some species. Specifically, if population density decreases below a critical threshold, extinction may be expedited, a phenomenon known as the Allee effect (Berec, Angulo & Courchamp 2007). Allee effects occur when individual fitness or population growth rates decrease below a given threshold (Berec, Angulo & Courchamp 2007). Species with complex social structures or those where social aggregation or information transfer improve fitness may be particularly vulnerable to Allee effects. For instance, in Vancouver Island marmots (*Marmota vancouverensis*) declining density and increased distance between neighboring social groups contributed to fewer social interactions and lower feeding rates because individual marmots increased vigilance, a behaviour which would have historically been shared among colony members (Brashares, Werner & Sinclair 2010). Incorporating Allee effects within the socioecological environment could yield critical insight into how social and spatial phenotypes respond to changes in population density.

In the context of framing socioecological environment within a broader conservation paradigm, HIREC reflects the habitat selection axis, while Allee effects reflect the social axis. Ultimately, HIREC and Allee effects are linked by density dependence; HIREC changes density, while Allee effects represent a response to changes in density. Understanding how *individuals* respond to HIREC, Allee effects and changes in density, in the context of the socioecological environment, could be a critical, yet under-appreciated aspect of how I apply conservation and management strategies.

Summary

We propose the social and ecological environments can be perceived as reflections of one another, linked by their density dependence, and interpreted as the socioecological environment. My conceptual framework outlines ecological and evolutionary analogies of social and spatial phenotypes and the likelihood of a socioecological behavioural syndrome. Components of the socioecological environment are density-dependent, and while I expect they are sufficiently plastic to respond to changes in density, they are also likely repeatable, thus meeting the criteria for individual animal personality traits. I also infer possible evolutionary outcomes associated with the socioecological environment by incorporating quantitative genetics. I suggest the heritability of components of social and spatial phenotypes are influenced by the phenotypes of conspecifics, particularly for fission-fusion societies, suggesting the importance of accounting for indirect genetic effects when estimating heritability. The socioecological environment concept shares many similarities with social and ecological niche theory, with an emphasis on the importance of fitness. Density-dependent social and spatial phenotypes, including niches, can therefore influence births and deaths, which

over a given timeframe can cumulatively affect individual fitness and its sum: dynamic population growth. Therefore, covariation in density-dependent individually consistent social and spatial behaviours and their adaptive value may explain variation in population dynamics. If social and spatial phenotypes are heritable and (co)vary across a population density gradient, their adaptive value is density-dependent, and if their distribution affects population dynamics, it may constitute an eco-evolutionary feedback or correlation (Pelletier, Garant, & Hendry, 2009; Smallegange & Coulson, 2013). Early evidence suggests that social and spatial phenotypes satisfy these conditions. Individual traits which respond to variation in the socioecological environment likely represent a density-dependent driver of fitness, population, and evolutionary dynamics.

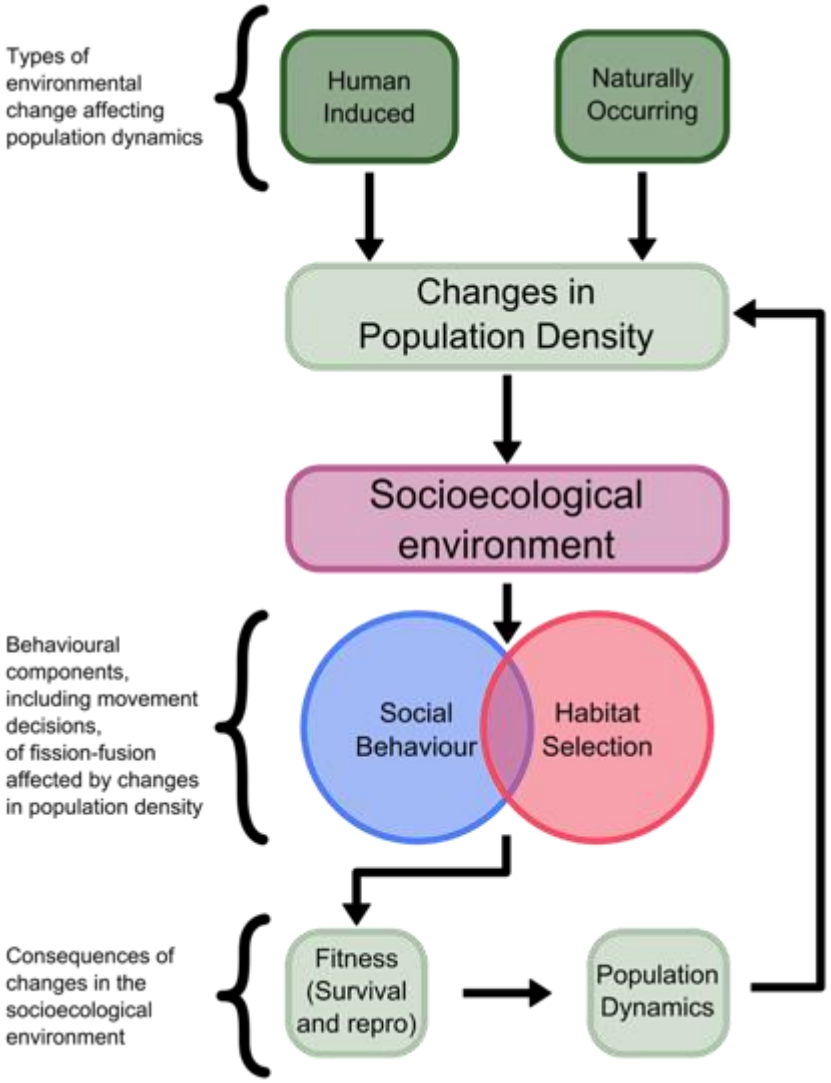
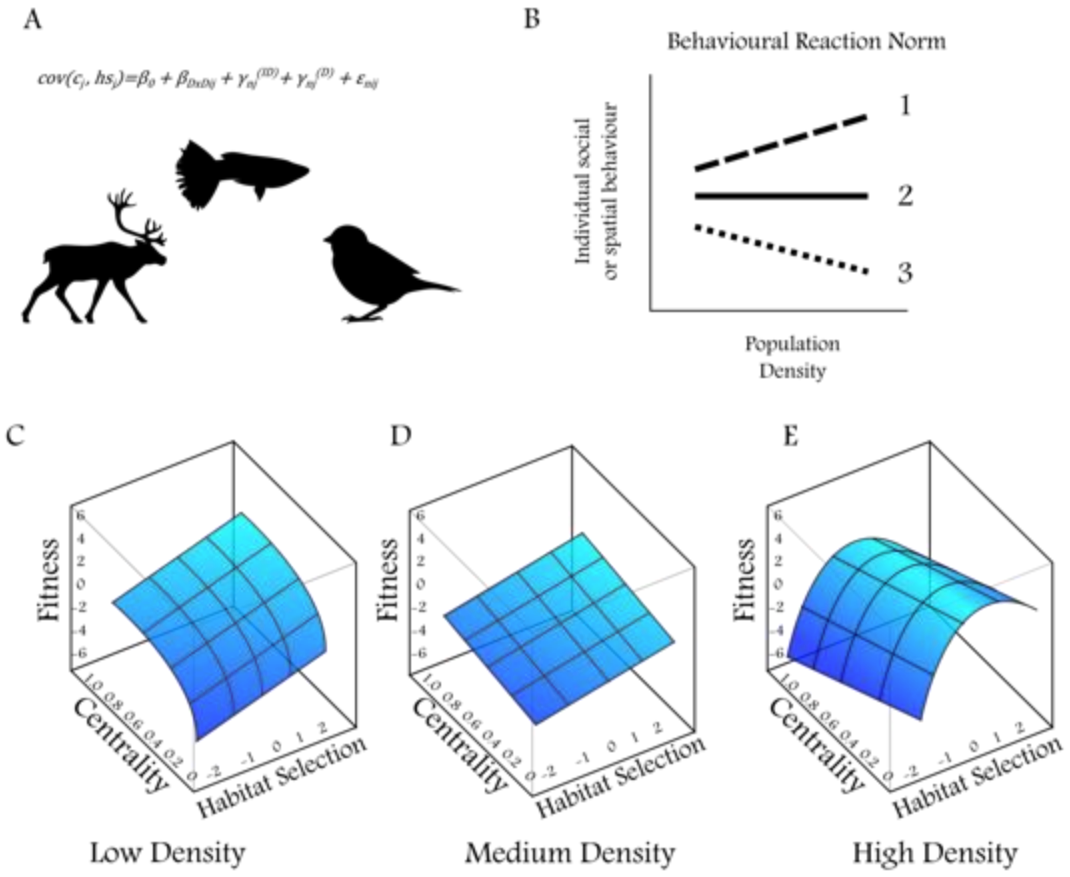


Figure 2.1: A simple conceptual framework to illustrate eco-evolutionary dynamics linking components of the socioecological environment and density. Here I illustrate how environmental changes, including naturally occurring and human induced, could affect population density, which drives changes in the socioecological environment through individual social behaviour and habitat selection. This subsequently could affect fitness (i.e., survival and reproduction) and population dynamics.



Box 2.1: Panel A) Possible applications of multivariate 'Animal Model' to quantify the socioecological environment. Covariance between individual values for social centrality (c_j) and habitat selection resource selection functions (hs_j) are modeled using a bivariate Animal Model framework (for details and tutorials on appropriate implementation see Houslay & Wilson 2017). Model slope (β_0) and density ($\beta_{DXD_{ij}}$) are included as fixed effects, while individual ID ($\Upsilon_{nj}^{(ID)}$) and density ($\Upsilon_{nj}^{(D)}$) are fit as random intercepts and slopes, enabling the model to be interpreted as a behavioural reaction norm (BRN: Dingemanse *et al.* 2010). This model could also include simple fixed effects, such as sex or year, while more complex extensions could include matrices of relatedness (i.e., pedigree), or a dyadic network (i.e., V_S). While the incorporation of pedigrees within the Animal Model is common, the use of dyadic social network matrices, instead of a

pedigree, is a potential tool which could account for variance in one or more response variables as a function of social network position. I note the inclusion of density as a fixed and random effect in my hypothetical 'Animal Model' framework fulfills two purposes: 1) inclusion as a fixed effect is to describe the *mean* change of the dependent variable(s); and 2) inclusion as a random effect is to describe *individual* deviation from the fixed effect mean, i.e., plasticity (Dingemanse, Barber, Wright, & Brommer, 2012).

Panel B) Variation in personality and plasticity can be captured by applying BRNs, which model individual differences (BRN intercept) in the plasticity (BRN slope) of a social or spatial phenotype across an environmental gradient, such as population density. My hypothetical BRN shows three possible scenarios. Variation in the intercepts of lines 1, 2, and 3 indicate individual differences in social or spatial behaviour in response to changes in population density, while the slopes of lines 1 and 3 represent two ways an individual (or population) could display plasticity, i.e., an Individual–Environment interaction, in response to changes in population density. If social or spatial traits are heritable, lines 1 and 3 represent a Genotype–Environment interaction (Nussey et al., 2007). Line 2 represents a scenario with no behavioural plasticity.

Panels C), D) and E) Hypothetical adaptive landscapes at three densities: low, medium, and high. Each landscape models the relationship between centrality (*c*) and habitat selection (*hs*) and estimates their covariance to produce an optimal fitness based on two predictions derived from (1) the social centrality hypothesis and (2) density-dependent habitat selection theory. 1) I predict that the benefit of being central will be higher at low density when competition for resources is lowest; whereas, as population density increases so too do the costs of competition with conspecifics. 2) Density-dependent

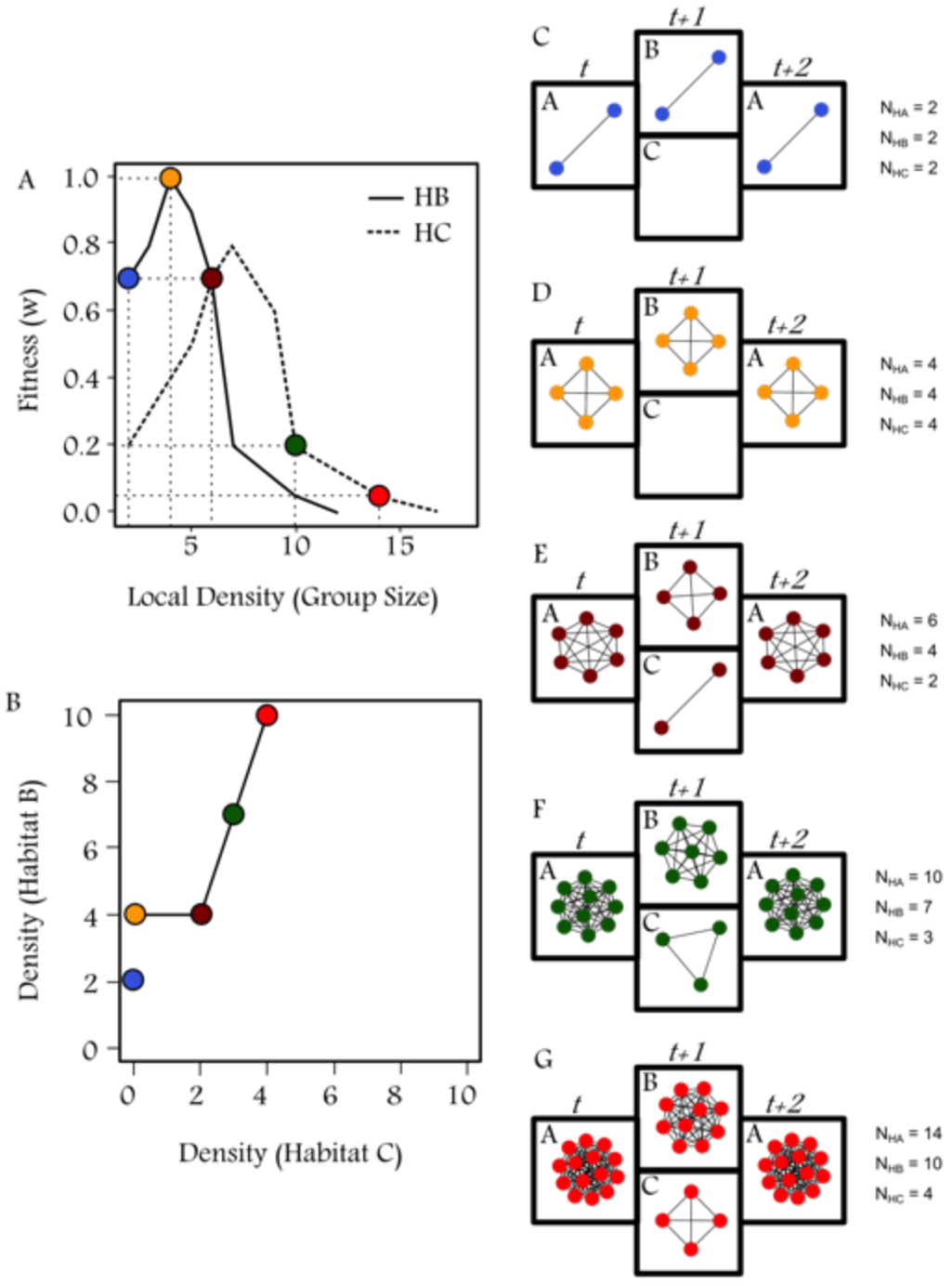
habitat selection predicts that at low density individuals will improve their fitness by being selective, i.e., resource specialists; whereas at higher density individuals should become resource generalists (Fortin et al., 2008).

Adaptive landscapes illustrate the covariance of traits which accord the highest fitness in light blue, while lowered fitness is denoted by darker blue segments. Values for habitat selection reflect an individual's selection (positive numbers) or avoidance (negative numbers) of specific habitats and values for centrality range from highly central (close to 1) to peripheral (close to 0). For each adaptive landscape, individual values of centrality and habitat selection at fitness optimum could be extracted and plotted across densities using the BRN approach to determine individual differences (intercept) and plasticity (slope).

Panel C) Adaptive landscape at low density yields highest fitness for individuals with high centrality that strongly select a given habitat, while fitness is lowest for individuals with low centrality that avoid that habitat.

Panel D) Adaptive landscape at medium density yields highest fitness for individuals that select a focal habitat, e.g., Habitat A from Box 2, and tend to be less social relative to low density, while fitness is lowest for individuals with higher centrality that avoid that habitat.

Panel E) Adaptive landscape at high density yields highest fitness for habitat generalists that have low centrality, while fitness is lowest for central individuals that select and avoid that habitat.



Box 2.2: Classic habitat selection theory is centered around the ideal free distribution (IFD) model where animals select habitat to maximize fitness (Fretwell & Lucas 1969). IFD theory posits, among other things, that habitat selection is density-dependent such that variation in density in different habitat patches leads to a fitness equilibrium

(Bradbury, Vehrencamp & Clifton 2015). Fitness in a habitat patch depends on density where, ideally, the available resources on a habitat patch can sustain a specific number of individuals. Extensions of IFD have yielded important contributions to habitat selection theory. Specifically, Morris (1987) developed 'isodar analysis' to model density-dependent habitat selection. Isodar analysis assumes that, in a finite world, fitness in a habitat declines after a critical threshold as a function of density (Morris 2011); unlike IFD, isodar theory does not have an assumption of proportionality, hence the non-linear relationship between fitness and density in Panel A. IFD theory has received extensive attention at the population-level (Morris 1987; 2003; 2011), despite the expectation that *individuals* are predicted to distribute themselves across habitats that accord the highest fitness. Indeed, IFD predicts that *mean* fitness in each habitat will be equal, implying that individual variation should still exist among individuals within each habitat.

Panel A) Distribution of fitness (w) values as a function of *overall* local density, which is analogous to group size, in two habitats (HB, sold line and HC, dashed line). Animals move from Habitat A (HA), a neutral starting point for my conceptual game, to HB and HC to equilibrate fitness (see below). Carrying capacity (K_i), i.e., the group size at which $w = 0$, for habitat B (K_{HB}) = 12, while $K_{HC} = 5$ (points at which solid (HB) and dashed (HC) habitat isoclines intersect and $w = 0$). Note, values of K were arbitrarily selected for this example. Each habitat has an optimal group size where mean fitness is maximized and the distributions of fitness represents a functional response to changes in local density for each habitat (Krause & Ruxton, 2002; Sibly, 1983). Coloured points represent one of five scenarios outlined in Panels C – G where a fission-fusion population with different starting densities moves through space. At low density (n < 4), fitness in HB >

fitness in HC, so individuals remain in a single group and enter HB as a single group (Panels C and D), a process which occurs up to a certain density threshold. Consistent with density-dependent habitat selection, this threshold is surpassed when isoclines for each habitat intersect, in this case n = 6 (Panel E). At this point, individuals begin to filter, i.e., fission, into HC where fitness is *equal* for individuals in HB and HC (Panels F and G), which can be visualized as an isodar (i.e., line of equal fitness) in Panel B. As dictated by density-dependent habitat selection, population density represents the *sum* of the values from the x-axis where fitness is equal in both habitats, so, for example, if local density is 10 individuals (green point), the first seven individuals will filter into HB and the next three individuals will filter into HC (Panel F). This generates a scenario where fitness is equal and can be visualized by following the horizontal dashed lines in Panel A (e.g., $w = 0.2$ from Panel A between habitats and the link between the isodar in Panel A and the fission-fusion diagram in Panel F is the *sum* of population densities in each habitat (7 and 3, respectively) where fitness is equal. Note: without the IFD assumption that habitats increase proportionally, the relationship between habitat and density is non-linear relationship in both habitats.

Panel B) The functional response observed in Panel A can be mapped using the logistic population growth function:

$$\frac{1}{N_i}\frac{dN_i}{dt} = r_i\left(1 - \frac{N_i}{K_i}\right) [Equation\ 4]$$

where N_i is the density of individuals in habitat i, r_i is the rate of population growth. Following *Equation 4*, a habitat isodar, i.e., the pair of local densities from HB and HC where fitness is equal, can be generated. In the two-habitat scenario described above, strategies are identified by the proportion (p) of individuals in HB ($0 \leq p \leq 1$), or

alternatively (q) the proportion of individuals in HC ($q = 1 - p$). Following Morris (2011), mean fitness for any strategy is:

$$p \cdot r_1\left(1 - \frac{N_1}{K_1}\right) + q \cdot r_2\left(1 - \frac{N_2}{K_2}\right) \; [Equation\ 5]$$

Equation 5 is the adaptive landscape of how fitness varies as a function of density-dependent habitat selection. The positive trend line through coloured points represents an isodar, which can be interpreted as the density in a pair of habitats where fitness is equal. Density-dependent habitat selection theory posits that individuals in a population will occupy a given habitat up to a certain density before filtering, or in this case fissioning, into a new habitat. Note: colours for each point represent scenarios outlined in Panels C – G.

Panels C – G) Schematic representation of fission-fusion dynamics for the same population of a hypothetical gregarious organism at different local densities in Habitat A across an initial time (*t*, left-hand boxes), second time step (*t +1*, centre boxes) and a final time step (*t + 2*, right-hand boxes). Time *t* reflects an ideal habitat patch, while time *t + 2* is a return to this patch via the patchy landscape displayed in time *t + 1*. These hypothetical scenarios were parameterized based on: 1) density-dependent habitat selection theory, which suggests that individuals occupy a given habitat up to a certain density at which point animals distribute themselves according to IFD (i.e., from HA to HB and HC); and 2) optimal group size theory, suggesting an optimal group size that maximizes fitness. Costs of sociality are predicted to increase more rapidly than the benefits, so the relationship between fitness and group size should be bell-shaped (Panel A).

Coloured nodes in each network represent individuals and each series of fission-fusion events begins at a given local density (2, 4, 6, 10, and 14, for each panel). I held individual centrality values equal across all networks, and individuals were never solitary because the hypothetical organism in my model is gregarious and, in my example, being solitary incurs a fitness value of zero. In each scenario three habitats (HA, light green boxes on left and right side of each diagram; HB, purple box on top; HC, light blue box on bottom) are represented. At time *t*, one of two events occur: 1) the group transitions form HA to HB as a fused unit (Panels C and D); or 2) the group fissions from HA to HB and HC (Panels E, F, and G). Groups remain fused in Panels C and D because fitness is higher if individuals stay together, while the groups fission in Panels E, F, and G to ensure mean fitness is equal between habitats.

Table 2.1: Summary of four hypotheses with associated predictions and empirical examples. These hypotheses could be tested in the context of the socioecological environment framework outlined in my conceptual synthesis.

Hypotheses	Associated Predictions	Example	References
Social Phenology Hypothesis	**P1:** Social interactions or aggregations will change across seasons in response to environmental variation.	In desert night lizards (*Xantusia vigilis*), social aggregation promotes social thermoregulation during winter, when ambient temperature is low, which confers an increase in reproductive success and survival among adult lizards.	Rabosky *et al.* (2012)
	P2: Social or socioecological decisions of an animal in one season will carry-over and enhance fitness in a subsequent season.	In great tits (*Parus major*), social foraging associations in winter carried over to spring territory establishment, where close associates in winter had adjacent territories in spring.	Firth & Sheldon (2016)
Social Assortment Hypothesis	**P1:** Individuals will actively assort through sexual segregation, where individuals tend to have stronger social associations with members of the same sex.	For ungulates, resource acquisition appears to drive sexual segregation because males and females vary in their activity levels, and thus energy-forage requirements. Females are expected to require higher quality forage, while males rely on lower quality, but higher quantity, of forage.	Ruckstuhl (2007)
	P2: Individuals will behaviourally assort according to variation in their personality traits. Behavioural assortment can be positive or negative.	In guppies (*Poecilia reticulata*) and three-spined stickleback (*Gasterosteus aculeatus*), individuals assorted based on the shy-bold personality axis, where shy fish had stronger, but fewer, social connections compared to bold fish, which had many weak social connections.	Pike *et al.* (2008); Croft *et al.* (2009)

Conspecific Attraction Hypothesis	**P1:** Individuals will use social information to make habitat searching and settlement decisions.	Least flycatchers (*Empidonax minimus*) used conspecific cues during habitat settlement regardless of patch size, suggesting flycatchers use social information to make decisions during habitat selection.	Fletcher (2009)
Resource Dispersion Hypothesis	**P1:** Territory size will be determined by dispersion of habitat patches with a given resource.	Dingo (*Canus lupus dingo*) territories were smaller when resources (food supplementation sites) were spatially aggregated on the landscape.	Newsome *et al.* (2013)

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2.7 References

Alexander, R. D. (1974). The evolution of social behavior. *Annual Review of Ecology, Evolution, and Systematics*, *5*, 325–383.

Aplin, L. M., Firth, J. A., Farine, D. R., Voelkl, B., Crates, R. A., Culina, A., … Sheldon, B. C. (2015). Consistent individual differences in the social phenotypes of wild great tits, *Parus major*. *Animal Behaviour*, *108*, 117–127. doi: 10.1016/j.anbehav.2015.07.016

Araújo, M. S., Bolnick, D. I., & Layman, C. A. (2011). The ecological causes of individual specialisation. *Ecology Letters*, *14*(9), 948–958. doi: 10.1111/j.1461-0248.2011.01662.x

Aureli, F., Schaffner, C. M., Boesch, C., Bearder, S. K., Call, J., Chapman, C. A., … Van Schaik, C. P. (2008). Fission-fusion dynamics: New research frameworks. *Current Anthropology*, *49*, 627–654. doi: 10.1086/586708

Avgar, T., Potts, J. R., Lewis, M. A., & Boyce, M. S. (2016). Integrated step selection analysis: Bridging the gap between resource selection and animal movement. *Methods in Ecology and Evolution*, *7*(5), 619–630. doi: 10.1111/2041-210X.12528

Banks, S. C., Lindenmayer, D. B., Wood, J. T., McBurney, L., Blair, D., & Blyton, M. D. J. (2013). Can Individual and Social Patterns of Resource Use Buffer Animal Populations against Resource Decline? *PLoS ONE*, *8*(1), e53672. doi: 10.1371/journal.pone.0053672

Basille, M., Calenge, C., Marboutin, E., Andersen, R., & Gaillard, J. M. (2008). Assessing habitat selection using multivariate statistics: Some refinements of the ecological-niche factor analysis. *Ecological Modelling*, *211*(1–2), 233–240. doi: 10.1016/j.ecolmodel.2007.09.006

Bell, A. M., Hankison, S. J., & Laskowski, K. L. (2009). The repeatability of behaviour: a meta-analysis. *Animal Behaviour*, *77*(4), 771–783. doi: 10.1016/j.anbehav.2008.12.022

Berec, L., Angulo, E., & Courchamp, F. (2007). Multiple Allee effects and population management. *Trends in Ecology and Evolution*, *22*(4), 185–191. doi: 10.1016/j.tree.2006.12.002

Bijma, P., & Wade, M. J. (2008). The joint effects of kin, multilevel selection and indirect genetic effects on response to genetic selection. *Journal of Evolutionary Biology*, *21*(5), 1175–1188. doi: 10.1111/j.1420-9101.2008.01550.x

Bolnick, D. I., Svanbäck, R., Fordyce, J. A., Yang, L. H., Davis, J. M., Hulsey, C. D., & Forister, M. L. (2003). The ecology of individuals: Incidence and implications of individual specialization. *The American Naturalist*, *161*(1), 1–28. doi: 10.1086/343878

Boon, A. K., Réale, D., & Boutin, S. (2007). The interaction between personality, offspring fitness and food abundance in North American red squirrels. *Ecology Letters*, *10*(11), 1094–1104. doi: 10.1111/j.1461-0248.2007.01106.x

Bradbury, J. W., Vehrencamp, S. L., & Clifton, K. E. (2015). The ideal free antelope: foraging dispersions. *Behavioral Ecology*, *arv078*, 1–11. doi: 10.1093/beheco/arv078

Brashares, J. S., Werner, J. R., & Sinclair, A. R. E. (2010). Social "meltdown" in the demise of an island endemic: Allee effects and the Vancouver Island marmot. *Journal of Animal Ecology*, *79*, 965–973. doi: 10.1111/j.1365-2656.2010.01711.x

Brent, L. J. N. (2015). Friends of friends: Are indirect connections in social networks important to animal behaviour? *Animal Behaviour*, *103*, 211–222. doi: 10.1016/j.anbehav.2015.01.020

Brommer, J. E. (2013). Phenotypic plasticity of labile traits in the wild. *Current Zoology*, *59*(4), 485–505. doi: 10.1093/czoolo/59.4.485

Croft, D. P., Krause, J., Darden, S. K., Ramnarine, I. W., Faria, J. J., & James, R. (2009). Behavioural trait assortment in a social network: Patterns and implications. *Behavioral Ecology and Sociobiology*, *63*(10), 1495–1503. doi: 10.1007/s00265-009-0802-x

Dantzer, B., Boutin, S., Humphries, M. M., & McAdam, A. G. (2012). Behavioral responses of territorial red squirrels to natural and experimental variation in population density. *Behavioral Ecology and Sociobiology*, *66*(6), 865–878. doi: 10.1007/s00265-012-1335-2

DeCesare, N. J., Hebblewhite, M., Bradley, M., Hervieux, D., Neufeld, L., & Musiani, M. (2014). Linking habitat selection and predation risk to spatial variation in survival. *Journal of Animal Ecology*, *83*(2), 343–352. doi: 10.1111/1365-2656.12144

DeWitt, T. J., Sih, A., & Wilson, D. S. (1998). Costs and limits of phenotypic plasticity. *Trends in Ecology and Evolution*, *13*, 77–81.

Dingemanse, N. J., & Araya-Ajoy, Y. G. (2015). Interacting personalities: Behavioural ecology meets quantitative genetics. *Trends in Ecology and Evolution*, *30*(2), 88–97. doi:

10.1016/j.tree.2014.12.002

Dingemanse, N. J., Barber, I., Wright, J., & Brommer, J. E. (2012). Quantitative genetics of behavioural reaction norms: Genetic correlations between personality and behavioural plasticity vary across stickleback populations. *Journal of Evolutionary Biology*, *25*(3), 485–496. doi: 10.1111/j.1420-9101.2011.02439.x

Dingemanse, N. J., Kazem, A. J. N., Réale, D., & Wright, J. (2010). Behavioural reaction norms: animal personality meets individual plasticity. *Trends in Ecology and Evolution*, *25*(2), 81–89. doi: 10.1016/j.tree.2009.07.013

Dochtermann, N. A., Schwab, T., & Sih, A. (2015). The contribution of additive genetic variation to personality variation: heritability of personality. *Proceedings of the Royal Society B*, *282*, 20142201. doi: 10.1098/rspb.2014.2201

Ellen, E. D., Peeters, K., Verhoeven, M., Gols, R., Harvey, J. A., Wade, M. J., … Bijma, P. (2016). Direct and indirect genetic effects in life-history traits of flour beetles (*Tribolium castaneum*). *Evolution*, *70*(1), 207–217. doi: 10.1111/evo.12835

Ezard, T. H. G., Côté, S. D., & Pelletier, F. (2009). Eco-evolutionary dynamics: disentangling phenotypic, environmental and population fluctuations. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, *364*(1523), 1491–1498. doi: 10.1098/rstb.2009.0006

Fagan, W. F., Lewis, M. A., Auger-Méthé, M., Avgar, T., Benhamou, S., Breed, G., … Mueller, T. (2013). Spatial memory and animal movement. *Ecology Letters*, *16*(10), 1316–1329. doi: 10.1111/ele.12165

Farine, D. R., Montiglio, P.-O., & Spiegel, O. (2015). From individuals to groups and back: The evolutionary implications of group phenotypic composition. *Trends in Ecology and Evolution*, *30*(10), 609–621.

Firth, J. A., & Sheldon, B. C. (2016). Social carry-over effects underpin trans-seasonally linked structure in a wild bird population. *Ecology Letters*, *19*, 1324–1332. doi: 10.1111/ele.12669

Fletcher, R. J. (2007). Species interactions and population density mediate the use of social cues for habitat selection. *Journal of Animal Ecology*, *76*(3), 598–606. doi: 10.1111/j.1365-2656.2007.01230.x

Fletcher, R. J. (2009). Does attraction to conspecifics explain the patch-size effect? An experimental test. *Oikos*, *118*(8), 1139–1147. doi: 10.1111/j.1600-0706.2009.17342.x

Fortin, D., Beyer, H. L., Boyce, M. S., Smith, D. W., Duchesne, T., & Mao, J. S. (2005). Wolves influence elk movements: Behavior shapes a trophic cascade in Yellowstone National Park. *Ecology*, *86*(5), 1320–1330.

Fortin, D., Fortin, M. E., Beyer, H. L., Duchesne, T., Courant, S., & Dancose, K. (2009). Group-size-mediated habitat selection and group fission-fusion dynamics of bison under predation risk. *Ecology*, *90*(9), 2480–2490. doi: 10.1890/08-0345.1

Fortin, D., Morris, D. W., & McLouglin, P. D. (2008). Habitat selection and the evolution of specialists in heterogeneous environments. *Israel Journal of Ecology & Evolution*, *54*(July), 295–309. doi: 10.1560/IJEE.54.3

Fretwell, S. D., & Lucas, H. L. J. (1969). On territorial behaviour and other factors influencing habitat distribution in birds. *Acta Biotheoretica*, *19*(1), 16–36. doi: 10.1007/BF01601953

Grabowska-Zhang, A. M., Wilkin, T. A., & Sheldon, B. C. (2011). Effects of neighbor familiarity on reproductive success in the great tit (*Parus major*). *Behavioral Ecology*, *23*(2), 322–333. doi: 10.1093/beheco/arr189

Hansen, T. F., Stenseth, N. C., Henttonen, H., & Tast, J. (1999). Interspecific and intraspecific competition as causes of direct and delayed density dependence in a fluctuating vole population. *Proceedings of the National Academy of Sciences*, *96*(986), 986–991. doi: 10.1073/pnas.96.3.986

Haydon, D. T., Morales, J. M., Yott, A., Jenkins, D. A., Rosatte, R., & Fryxell, J. M. (2008). Socially informed random walks: incorporating group dynamics into models of population spread and growth. *Proceedings of the Royal Society B*, *275*(1638), 1101–1109. doi: 10.1098/rspb.2007.1688

Hendry, A. P., Kinnison, M. T., Heino, M., Day, T., Smith, T. B., Fitt, G., … Carroll, S. P. (2011). Evolutionary principles and their practical application. *Evolutionary Applications*, *4*(2), 159–183. doi: 10.1111/j.1752-4571.2010.00165.x

Hirsch, B. T. (2007). Costs and benefits of within-group spatial position: a feeding competition model. *The Quarterly Review of Biology*, *82*(1), 9–27.

Hofmann, H. A., Beery, A. K., Blumstein, D. T., Couzin, I. D., Earley, R. L., Hayes, L. D., … Rubenstein, D. R. (2014). An evolutionary framework for studying mechanisms of social behavior. *Trends in Ecology & Evolution*, *29*(10), 1–9. doi: 10.1016/j.tree.2014.07.008

Houslay, T. M., & Wilson, A. J. (2017). Avoiding the misuse of BLUP in behavioural ecology. *Behavioral Ecology*, *28*, 948–952. doi: 10.1093/beheco/arx023

Krause, J., James, R., & Croft, D. P. (2010). Personality in the context of social networks. *Philosophical Transactions of the Royal Society B*, *365*(1560), 4099–4106. doi: 10.1098/rstb.2010.0216

Krause, J., & Ruxton, G. D. (2002). *Living in groups*. Oxford University Press.

Laskowski, K.L., Montiglio, P.-O., & Pruitt, J. N. (2016). Individual and group performance

suffers from social niche disruption. *The American Naturalist*, *187*(6), 776–785. doi: 10.1086/686220

Laskowski, K.L., Montiglio, P.-O., & Pruitt, J. N. (2020). Retraction: "Individual and group performance suffers from social niche disruption." *American Naturalist*, *195*(2), 393. doi: 10.1086/708066

Laskowski, K.L, & Pruitt, J. N. (2014). Evidence of social niche construction: persistent and repeated social interactions generate stronger personalities in a social spider. *Proceedings of the Royal Society B*, *281*(1783), 20133166. doi: 10.1098/rspb.2013.3166

Laskowski, Kate L., Modlmeier, A. P., DeMarco, A. E., Coleman, A., Zhao, K., Brittingham, H. A., … Pruitt, J. N. (2014). Retraction: Persistent social interactions beget more pronounced personalities in a desert-dwelling social spider. *Biology Letters*, *10*(8), 20200062. doi: 10.1098/rsbl.2014.0419

Laskowski, Kate L., & Pruitt, J. N. (2014). Retraction: Evidence of social niche construction: Persistent and repeated social interactions generate stronger personalities in a social spider. *Proceedings of the Royal Society B: Biological Sciences*, *281*(1783), 2020. doi: 10.1098/rspb.2013.3166

Leclerc, M., Vander Wal, E., Zedrosser, A., Swenson, J. E., Kindberg, J., & Pelletier, F. (2016). Quantifying consistent individual differences in habitat selection. *Oecologia*, *180*, 697–705. doi: 10.1007/s00442-015-3500-6

Manly, B. F. J., McDonald, L. L., Thomas, D. L., McDonald, T. L., & Erickson, W. P. (2002). *Resource selection by animals: statistical design and analysis for field studies* (2nd Editio). Dordrecht: Kluwer Academic.

Mathot, K.J., Wright, J., Kempenaers, B., & Dingemanse, N. J. (2012). Adaptive strategies for managing uncertainty may explain personality-related differences in behavioural plasticity. *Oikos*, *121*(7), 1009–1020. doi: 10.1111/j.1600-0706.2012.20339.x

Mathot, Kimberley J, & Dingemanse, N. J. (2015). Animal personality: moving beyond optimality and embracing individual differences. In L. B. Martin, C. K. Ghalambor, & H. . Woods (Eds.), *Integrative Organismal Biology, First Edition* (pp. 55–69). John Wiley & Sons Inc.

Matthiopoulos, J., Fieberg, J., Aarts, G., Beyer, H. L., Morales, J. M., & Haydon, D. T. (2015). Establishing the link between habitat selection and animal population dynamics. *Ecological Monographs*, *85*(3), 413–436. doi: 10.1890/14-2244.1

McLoughlin, P. D., Boyce, M. S., Coulson, T., & Clutton-Brock, T. (2006). Lifetime reproductive success and density-dependent, multi-variable resource selection. *Proceedings of the Royal Society B*, *273*(1593), 1449–1454. doi: 10.1098/rspb.2006.3486

McLoughlin, P. D., Morris, D. W., Fortin, D., Vander Wal, E., & Contasti, A. L. (2010). Considering ecological dynamics in resource selection functions. *Journal of Animal Ecology*, *79*(1), 4–12. doi: 10.1111/j.1365-2656.2009.01613.x

Merkle, J. A., Sigaud, M., & Fortin, D. (2015). To follow or not? How animals in fusion-fission societies handle conflicting information during group decision-making. *Ecology Letters*, *18*(8), 799–806. doi: 10.1111/ele.12457

Modlmeier, A. P., Laskowski, K. L., DeMarco, A. E., Coleman, A., Zhao, K., Brittingham, H. A., … Pruitt, J. N. (2014). Persistent social interactions beget more pronounced personalities in a desert-dwelling social spider. *Biology Letters*, *10*(8), 20140419. doi: 10.1098/rsbl.2014.0419

Montiglio, P.-O., Ferrari, C., & Réale, D. (2013). Social niche specialization under constraints: personality, social interactions and environmental heterogeneity. *Philosophical Transactions of the Royal Society B*, *368*(1618), 20120343. doi: 10.1098/rstb.2012.0343

Montiglio, P.-O., Garant, D., Bergeron, P., Messier, G. D., & Reale, D. (2014). Pulsed resources and the coupling between life-history strategies and exploration patterns in eastern chipmunks (*Tamias striatus*). *Journal of Animal Ecology*, *83*, 720–728. doi: 10.1111/1365-2656.12174

Morris, D. W. (1987). Tests of density-dependent habitat selection in a patchy environment. *Ecological Monographs*, *57*(4), 269–281.

Morris, D. W. (2003). Toward an ecological synthesis: A case for habitat selection. *Oecologia*, *136*(1), 1–13. doi: 10.1007/s00442-003-1241-4

Morris, D. W. (2011). Adaptation and habitat selection in the eco-evolutionary process. *Proceedings of the Royal Society B*, *278*(1717), 2401–2411. doi: 10.1098/rspb.2011.0604

Naud, A., Chailleux, E., Kestens, Y., Bret, C., Desjardins, D., Petit, O., … Sueur, C. (2016). Relations between spatial distribution, social affiliations and dominance hierarchy in a semi-free mandrill population. *Frontiers in Psychology*, *7*(May), 1–11. doi: 10.3389/fpsyg.2016.00612

Newsome, T. M., Ballard, G.-A., Dickman, C. R., Fleming, P. J. S., & van de Ven, R. (2013). Home range, activity and sociality of a top predator, the dingo: a test of the Resource Dispersion Hypothesis. *Ecography*, *36*(8), 914–925. doi: 10.1111/j.1600-0587.2013.00056.x

Nussey, D. H., Wilson, A. J., & Brommer, J. E. (2007). The evolutionary ecology of individual phenotypic plasticity in wild populations. *Journal of Evolutionary Biology*, *20*(3), 831–844. doi: 10.1111/j.1420-9101.2007.01300.x

Pelletier, F., Garant, D., & Hendry, A. P. (2009). Eco-evolutionary dynamics. *Philosophical*

Transactions of the Royal Society B, *364*(1523), 1483–1489. doi: 10.1098/rstb.2009.0027

Pettorelli, N., Coulson, T., Durant, S. M., & Gaillard, J.-M. (2011). Predation, individual variability and vertebrate population dynamics. *Oecologia*, *167*(2), 305–314.

Pike, T. W., Madhumita, S., Lindström, J., & Royle, N. J. (2008). Behavioural phenotype affects social interactions in an animal network. *Proceedings of the Royal Society B*, *275*(1650), 2515–2520. doi: 10.1098/rspb.2008.0744

Pruitt, J.N., Bolnick, D. I., Sih, A., Dirienzo, N., & Pinter-wollman, N. (2016). Behavioural hypervolumes of spider communities predict community performance and disbandment. *Proceedings of the Royal Society B*, *283*, 20161409.

Pruitt, J.N., Howell, K. A., Gladney, S. J., Yang, Y., Lichtenstein, J. L. L., Spicer, M. E., … Pinter-Wollman, N. (2017). Behavioral hypervolumes of predator groups and predator-predator interactions shape prey survival rates and selection on prey behavior. *The American Naturalist*, *189*(3), 254–266. doi: 10.1086/690292

Pruitt, Jonathan N., Bolnick, D. I., Sih, A., DiRienzo, N., & Pinter-Wollman, N. (2016). Authorship removal correction for "Behavioural hypervolumes of spider communities predict community performance and disbandment." *Proceedings of the Royal Society B: Biological Sciences*, *283*(1844), 2020. doi: 10.1098/rspb.2016.1409

Rabosky, A. R. D., Corl, A., Liwanag, H. E. M., Surget-Groba, Y., & Sinervo, B. (2012). Direct fitness correlates and thermal consequences of facultative aggregation in a desert lizard. *PLoS ONE*, *7*(7). doi: 10.1371/journal.pone.0040866

Ruckstuhl, K. E. (2007). Sexual segregation in vertebrates: Proximate and ultimate causes. *Integrative and Comparative Biology*, *47*(2), 245–257. doi: 10.1093/icb/icm030

Saltz, J. B., Geiger, A. P., Anderson, R., Johnson, B., & Marren, R. (2016). What, if anything, is a social niche? *Evolutionary Ecology*, *30*(2), 349–364. doi: 10.1007/s10682-015-9792-5

Seyfarth, R. M., & Cheney, D. L. (2015). Social cognition. *Animal Behaviour*, *103*, 191–202. doi: 10.1016/j.anbehav.2015.01.030

Sibly, R. M. (1983). Optimal group size is unstable. *Animal Behaviour*, *31*(3), 947–948.

Sigaud, M., Merkle, J. A., Cherry, S. G., Fryxell, J. M., Berdahl, A., & Fortin, D. (2017). Collective decision-making promotes fitness loss in a fusion-fission society. *Ecology Letters*, *20*, 33–40. doi: 10.1111/ele.12698

Sih, A. (2013). Understanding variation in behavioural responses to human-induced rapid environmental change: A conceptual overview. *Animal Behaviour*, *85*(5), 1077–1088. doi: 10.1016/j.anbehav.2013.02.017

Sih, A., Bell, A. M., Johnson, J. C., & Ziemba, A. R. E. (2004). Behavioural syndromes: an integrative overview. *The Quarterly Review of Biology*, *51*(2), 211–244. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/785523

Sih, A., Cote, J., Evans, M., Fogarty, S., & Pruitt, J. (2012). Ecological implications of behavioural syndromes. *Ecology Letters*, *15*(3), 278–289. doi: 10.1111/j.1461-0248.2011.01731.x

Sih, A., Ferrari, M. C. O., & Harris, D. J. (2011). Evolution and behavioural responses to human-induced rapid environmental change. *Evolutionary Applications*, *4*(2), 367–387. doi: 10.1111/j.1752-4571.2010.00166.x

Silk, J. B. (2007). The adaptive value of sociality in mammalian groups. *Philosophical Transactions of the Royal Society B*, *362*(1480), 539–559. doi: 10.1098/rstb.2006.1994

Silk, M. J., Croft, D. P., Tregenza, T., & Bearhop, S. (2014). The importance of fission–fusion social group dynamics in birds. *Ibis*, *156*, 701–715.

Smallegange, I. M., & Coulson, T. (2013). Towards a general, population-level understanding of eco-evolutionary change. *Trends in Ecology and Evolution*, *28*(3), 143–148. doi: 10.1016/j.tree.2012.07.021

Smith, J. E., Kolowski, J. M., Graham, K. E., Dawes, S. E., & Holekamp, K. E. (2008). Social and ecological determinants of fission-fusion dynamics in the spotted hyaena. *Animal Behaviour*, *76*(3), 619–636. doi: 10.1016/j.anbehav.2008.05.001

Soberón, J. (2007). Grinnellian and Eltonian niches and geographic distributions of species. *Ecology Letters*, *10*(12), 1115–1123. doi: 10.1111/j.1461-0248.2007.01107.x

Spiegel, O., & Crofoot, M. C. (2016). The feedback between where we go and what we know—information shapes movement, but movement also impacts information acquisition. *Current Opinion in Behavioral Sciences*, *12*, 90–96. doi: 10.1016/j.cobeha.2016.09.009

Sueur, C., King, A. J., Conradt, L., Kerth, G., Lusseau, D., Mettke-Hofmann, C., … Aureli, F. (2011). Collective decision-making and fission-fusion dynamics: A conceptual framework. *Oikos*, *120*(11), 1608–1617. doi: 10.1111/j.1600-0706.2011.19685.x

Trainor, A. M., & Schmitz, O. J. (2014). Infusing considerations of trophic dependencies into species distribution modelling. *Ecology Letters*, *17*, 1507–1517. doi: 10.1111/ele.12372

Tuomainen, U., & Candolin, U. (2011). Behavioural responses to human-induced environmental change. *Biological Reviews*, *86*(3), 640–657. doi: 10.1111/j.1469-185X.2010.00164.x

van Beest, F. M., Uzal, A., Vander Wal, E., Laforge, M. P., Contasti, A. L., Colville, D., & Mcloughlin, P. D. (2014). Increasing density leads to generalization in both coarse-grained habitat selection and fine-grained resource selection in a large mammal. *Journal of Animal*

Ecology, *83*(1), 147–156. doi: 10.1111/1365-2656.12115

Vander Wal, E., Festa-Bianchet, M., Réale, D., Coltman, D. W., & Pelletier, F. (2015). Sex-based differences in the adaptive value of social behavior contrasted against morphology and environment. *Ecology*, *96*(3), 631–641. doi: 10.1890/14-1320.1.sm

Vander Wal, E., Garant, D., Festa-Bianchet, M., & Pelletier, F. (2013). Evolutionary rescue in vertebrates: evidence, applications and uncertainty. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, *368*(1610), 20120090. doi: 10.1098/rstb.2012.0090

Vander Wal, E., Yip, H., & McLoughlin, P. D. (2012). Sex-based differences in density-dependent sociality: An experiment with a gregarious ungulate. *Ecology*, *93*(1), 206–212. doi: 10.1890/11-0020.1

Wey, T., Blumstein, D. T., Shen, W., & Jordán, F. (2008). Social network analysis of animal behaviour: a promising tool for the study of sociality. *Animal Behaviour*, *75*(2), 333–344. doi: 10.1016/j.anbehav.2007.06.020

Wilson, A. D. M., Krause, S., Dingemanse, N. J., & Krause, J. (2013). Network position: A key component in the characterization of social personality types. *Behavioral Ecology and Sociobiology*, *67*(1), 163–173. doi: 10.1007/s00265-012-1428-y

Wilson, A. J., Gelin, U., Perron, M.-C., & Réale, D. (2009). Indirect genetic effects and the evolution of aggression in a vertebrate system. *Proceedings of the Royal Society B*, *276*(1656), 533–541. doi: 10.1098/rspb.2008.1193

Wolf, M., van Doorn, G. S., & Weissing, F. J. (2008). Evolutionary emergence of responsive and unresponsive personalities. *Proceedings of the National Academy of Sciences*, *105*(41), 15825–15830.

Wolf, M., & Weissing, F. J. (2010). An explanatory framework for adaptive personality differences. *Philosophical Transactions of the Royal Society B*, *365*(1560), 3959–3968. doi: 10.1098/rstb.2010.0215

CHAPTER 3:MOVING TOGETHER, FORAGING APART: EFFECTS OF THE SOCIAL ENVIRONMENT ON MOVEMENT-INTEGRATED HABITAT SELECTION

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3.1 Abstract

Movement links the distribution of habitats and the social environment of animals that select those habitats; yet integrating movement, habitat selection, and socioecology remains an opportunity. Here, my objective was to disentangle the roles of habitat selection and social association as drivers of collective movement in caribou (*Rangifer tarandus*). To accomplish this objective I: (1) assessed whether socially familiar individuals form discrete social communities and whether social communities have high spatial, but not necessarily temporal, overlap; and (2) modelled the relationship between collective movement and selection of foraging habitats using socially informed integrated step selection analysis. Based on assignment of individuals to social communities and home range overlap analyses, individuals assorted into discrete social communities and these communities had high spatial overlap. By unifying social network analysis and movement ecology, I identified state-dependent social association, where individuals were less cohesive when foraging, but were cohesive and moved collectively between foraging patches. My study demonstrates that social behaviour and space use are inter-related based on spatial overlap of social communities and state-dependent habitat selection. Movement, habitat selection, and social behaviour are linked in theory and practice and here I demonstrate that movement is the glue connecting individual habitat selection to the social environment.

Keywords: caribou, integrated step selection analysis, movement ecology, social preference, social network analysis

3.2 Introduction

Movement is defined by a change in spatial location and is described as the behavioural link between the physical space an animal occupies and the resources available to them (Van Moorter et al. 2016). In the context of the social environment, movement represents the connection between the distribution of resources and the social structure of animals that consume those resources (He et al. 2019). Disentangling the social and spatial drivers of movement is a formidable challenge within behavioural ecology and in many cases the social contexts within which animals move to, from, and within the areas that contain resources are often omitted (but see Spiegel et al. 2018; Strandburg-Peshkin et al. 2018). Spatially-explicit models of sociality highlight that some gregarious species aggregate at areas associated with profitable resources (Chamaillé-Jammes et al. 2008), while territorial species typically only interact at territory edges (Spiegel et al. 2018). Sharing space, either at resources, territory edges, or elsewhere within an animal's range, is required to form the social environment, and movement is required to access resources. For example, animals are predicted to select habitat as a function of the profitability and availability of the habitat (van Beest et al. 2014). A logical extension can be made to conspecifics; individuals form groups based on their familiarity with conspecifics. I aim to quantify the relative importance of habitat and conspecifics by developing a socially informed integrated step selection analysis, a movement-based method that accounts for the relative intensity of selection for habitats and neighbours.

For social animals, movement shapes social encounters and subsequent interactions with conspecifics and can affect collective movement (Jolles et al. 2019). Further complicating my understanding of collective movement is the notion that the type, quality, and distribution of habitats on the landscape can constrain or promote collective movement (Strandburg-Peshkin et

al. 2017). For example, dense vegetation impedes visibility, which could reduce the probability a group remains together. In addition, individual movement and habitat selection are affected by the distribution of resources, for example, patchily distributed resources could facilitate large aggregations, whereas homogenously distributed resources could result in a reduction in social associations (Spiegel et al. 2017). The physical space an individual, or group, occupies and the distribution and availability of resources within that space are important drivers of animal movement and the social environment an individual experiences (He et al. 2019).

Animals typically select habitat to optimize the trade-off between foraging and risk of predation. Benefits of grouping are that information transfer about foraging is assumed to be greater in open areas and the per capita risk of predation is lower (Lima 1995). For example, animals in larger groups reduce time spent vigilant, but also the per capita risk of being predated (Creel et al. 2014). However, not all social groups are equal; some groups contain unfamiliar individuals (Harel et al. 2017) while others contain familiar individuals (Lachlan et al. 1998). For both unfamiliar and familiar groups, social foraging occurs when the costs and benefits of an individual's foraging behaviour are linked with the foraging behaviour of conspecifics (Giraldeau and Dubois 2008). However, social foraging can be most beneficial when social information about resources comes from familiar individuals (Patin et al. 2019). For example, when foraging resources are unpredictable, familiar individuals obtain reliable information from conspecifics to increase foraging efficiency (Spiegel and Crofoot 2016; Jones et al. 2020), such that time searching for forage is reduced in favour of more time spent foraging. In the context of movement and habitat selection, theory on social foraging and the benefits of social familiarity provides a framework through which the costs and benefits of collective movement can be explored (Giraldeau and Dubois 2008; Giraldeau and Caraco 2018).

Apparent social familiarity or preference is the long-term repeated social association due to shared space at the same time. Although individuals often interact with many conspecifics, non-random repeated social interactions or associations with certain individuals form the basis for social preference (Mourier et al. 2012). Proximately, long-term social relationships can influence collective movement via the reliability of information transfer about foraging resources or predator risk (Best et al. 2013; Muller et al. 2018), while ultimately they can enhance fitness (Silk 2007). The social environment can be influenced by the availability and distribution of resources, but social communities could also be composed of individuals with similar physiological or nutritional requirements that occupy the same locations. Apparent social preference may therefore arise as a function of spatial constraints (Spiegel et al. 2016), including physical barriers, such as rivers or mountains. Disentangling social preference from spatial constraint could inform our understanding of collective movement and habitat selection (Pinter-Wollman et al. 2013; Croft et al. 2016).

Here, I develop a unified framework to bridge the gap between social network analysis and movement ecology. I disentangle the roles of social preference and collective movement on habitat selection behaviour by parameterizing socially informed integrated step selection models (Figure 3.1). Animal social networks often comprise distinct sub-networks, or social communities, defined by the existence of social preference among discrete clusters of individuals (Mourier et al. 2012). Using a social ungulate as a model system, my objective was to disentangle the roles of habitat selection and social association as drivers of collective movement in a gregarious ungulate (*Rangifer tarandus*) when the availability and distribution of foraging resources are variable. I calculated three distinct measures of social preference. First, I assigned individuals to social communities based on a community detection algorithm. Second, I assessed

the temporal stability of social association among individuals. Third, I estimated spatial overlap of social communities using home range analyses. Due to variance in the distribution of foraging resources on the landscape, I expected that access to social information via close proximity to conspecifics and collective movement should influence patterns of selection for foraging resources. Specifically, individuals with stronger social preference should select foraging habitat collectively. The corollary is that individuals should also take short steps in the presence of conspecifics, given that from a movement ecology perspective, shorter steps typically represent foraging behaviour and longer steps represent searching behaviour (Owen-Smith et al. 2010).

3.3 Materials and Methods

3.3.1 Caribou as a model system

We investigated patterns of movement, space use, and social behaviour for caribou (*Rangifer tarandus*) on Fogo Island, Newfoundland, Canada. Fogo Island is a small (~237km^2) island off the northeastern coast of Newfoundland with a humid continental climate (see Supplementary Materials S2 for details). Between 1964-1967, 26 caribou were introduced to Fogo Island from the Island of Newfoundland (Bergerud and Mercer 1989). Currently, Fogo Island has a population of approximately 300 caribou (Newfoundland and Labrador Wildlife Division, unpublished data). Caribou live in fission-fusion societies (Lesmerises et al. 2018) and throughout much of their range caribou forage primarily on lichen, grasses, sedges, and other deciduous browse with access to these resources changing between the seasons (Bergerud 1974). During winter (January–March) the landscape is covered by snow, and caribou forage primarily on lichen. Lichen is heterogeneously distributed and access is impeded by snow and ice cover. Caribou dig holes in the snow, termed craters, to access lichen in the winter. Caribou crater where snow depth is relatively shallow (ca. 30–60 cm deep). Consequently, caribou have limited

access to subnivean forage and tend to re-use established craters. To cope with this limitation, caribou use conspecific attraction and social information transfer to gain access to foraging opportunities in winter (Peignier et al. 2019). In winter, caribou activity budgets suggest that caribou spend approximately 50% of their time foraging, while approximately 40% of their time is spent lying down or ruminating, 7% of their time is spent walking or trotting, and 3% of their time is spent standing (Boertje 1985; Duquette and Klein 1987). In addition, caribou typically avoid forested habitats due to the presence of deep snow and lack of access to forage opportunities (Fortin et al. 2008), whereas most open habitats on Fogo Island are windswept in the winter, therefore facilitating foraging and movement (Bergerud 1974).

We used GPS location data collected from Fogo Island caribou (2017–2019) to assess the relationship between social behaviour, habitat selection, and movement (see supplementary information S2 for details on collaring procedures). Each relocation was assigned to a given habitat classification that was extracted from Landsat images with 30x30m pixels (Lewis 2014). Locations were categorized as one of open foraging (lichen barrens), open moving (wetland, rocky outcrops, and water/ice), or closed (conifer scrub, mixed wood, and conifer forest). Adult female caribou (n = 26 individual caribou, n = 72 caribou-years) were immobilized and fitted with global positioning system (GPS) collars (Lotek Wireless Inc., Newmarket, ON, Canada, GPS4400M collars, 1,250 g). Collars had 2 hour fix rates and prior to analyses, I removed all erroneous and outlier GPS locations following Bjørneraas et al. (2010). Specifically, I removed outlier GPS locations were recorded in unrealistic locations, relocations in the ocean, and relocations that were associated with step lengths exceeding the size of Fogo Island (30km). I did not collar all female caribou in the herd, however, and collared individuals were randomly selected from the population. I therefore assume that my sample of collared animals was

randomly distributed. Although associations between collared and uncollared animals were unrecorded, I assumed that my networks (see below) were unbiased representations of the relative degree of social association among all caribou.

3.3.2 Formulating integrated step selection models

Integrated step selection analysis (iSSA) simultaneously incorporates movement and habitat selection within a conditional logistic regression framework (Figure 3.1; Avgar et al. 2016). As in other resource and step selection analyses (Fortin et al. 2005), iSSA models habitat use as a binomial response variable where 'use' represents the location an animal was observed and 'availability' represents the geographical area an animal could potentially use but was not necessarily observed (Figure 3.2). iSSA defines availability based on empirically fitted distributions of step lengths and turn angles (Avgar et al. 2016), where a step is the linear connection between consecutive relocations, and turn angle is the angular deviation between the headings of two consecutive steps (Prokopenko et al. 2017). I generated available steps and turn angles based on the distributions informed by observed population-level movement behaviour using the *amt* package in R (Signer et al. 2019). First, I sampled step lengths from a gamma distribution of observed step lengths for the study population; values were log-transformed for analysis. The statistical coefficient of log-transformed step length is a modifier of the shape parameter from the gamma distribution originally used to generate available steps (Avgar et al. 2016). Second, I sampled turn angles (measured in radians) for available steps from observed values between $-\pi$ and π following a Von Mises distribution; values were cosine transformed for analysis. The statistical coefficient of cosine transformed turn angle is an unbiased estimator of the concentration parameter of the Von Mises distribution (Duchesne et al. 2015; Avgar et al. 2016). Each observed relocation was paired through a shared start point with 10 available steps

generated from step-length and turn-angle distributions and compared in a conditional logistic regression framework (see section 3.3.7).

3.3.3 Social network analysis

We used the R (R Core Team 2019) package *spatsoc* (Robitaille et al. 2019) to generate proximity-based social association networks from GPS location data. Nodes in the networks were represented by individual caribou and edges were represented by the frequency of association based on proximity between individuals. I generated social networks at two scales based on proximity of locations for individual caribou: (1) seasonal winter networks to assign individuals to social communities and assess long-term social preference and (2) weekly networks to assess the role of short-term social preference on patterns of habitat selection (see above). For networks at both seasonal and weekly scales, I assumed association between two individuals when simultaneous locations (i.e. GPS relocations that were meant to occur on the 2 h mark, but erroneously occurred within 5 min of the intended 2 h relocation) were within 50 m of one another (Lesmerises et al. 2018; Peignier et al. 2019). I selected the 50 m threshold based on the standard distance applied to assign individuals to groups in studies of ungulate group size and social behaviour (Kasozi and Montgomery 2020). I applied the 'chain rule', where each discrete GPS fix was buffered by 50 m, and I considered individuals in the same group if 50 m buffers for two or more individuals were contiguous, even if some individuals were beyond 50 m of one another. I weighted edges of social networks by the strength of association between dyads of caribou using the simple ratio index (Cairns and Schwager 1987), SRI:

$$SRI = \frac{x}{x + y_{AB} + y_A + y_B}$$

where x is the number of times individuals A and B were within 50 m of each other, y_A is the number of fixes from individual A when individual B did not have a simultaneous fix (i.e. within

5 min), y_B is the number of fixes from individual B when individual A did not have a simultaneous fix, and y_{AB} is the number of simultaneous fixes from individuals A and B that were separated by >50 m (Farine and Whitehead 2015). I constructed social networks with the *igraph* package in R (Csárdi and Nepusz 2006). Nodes in my networks therefore represented individuals and edges represented associations between individuals.

3.3.4 Detecting social communities: long-term social preference

For seasonal winter social networks, I used a community detection algorithm to define social communities (Newman 2006). Social communities represent a subset of individuals within a network that are more closely connected with each other than with the rest of the network. I assessed social community structure for each winter to determine the broadest extent of social structure. Modularity is a commonly used measure that defines how well-connected social communities are to one another. It is calculated from the weighted proportion of edges that occur within a community, minus the expected proportion of edges, if edges were distributed randomly in the network (Newman 2006). A modularity value close to 1 indicates a network with a strong clustered structure in which interactions of individuals belonging to different clusters do not occur. I quantified modularity (Q) for observed annual winter networks. To ensure observed social structure did not occur at random, I compared these values to null models (Spiegel et al. 2016). Specifically, I generated null models based on GPS fixes to reduce potential for type II error typically associated with node-based permutations (Farine 2014). Following Spiegel et al. (Spiegel et al. 2016), I re-ordered daily GPS movement trajectories for each individual while maintaining the temporal path sequence within each time block (e.g., day 1 and day 2 may be swapped). This technique is a robust network randomization procedure for GPS data because: 1) it maintains the spatial aspects of an individual's movement; and 2) by randomizing movement

trajectories of individuals independent of one another, temporal dependencies of movement are decoupled (Spiegel et al. 2016). I repeated this procedure 100 times for annual winter networks and re-calculated modularity at each iteration. I then compared observed modularity (*Q*) values to the null distribution and determined whether the observed *Q* value fell within the 95% confidence interval of the distribution of *Q* values (Mourier et al. 2012).

In addition to comparing observed *Q* values from annual winter networks to a null distribution, I also calculated a community assortativity coefficient (R_{com}) to assess confidence in the assignment of an individual to a given community (Shizuka and Farine 2016). Specifically, $R_{com} = 0$ indicates no confidence in the assignment of an individual to a community, while $R_{com} = 1$ indicates certainty in the assignment of an individual to its community.

3.3.5 Weekly networks and lagged association rates: short-term social preference

We iteratively generated weekly social networks using a moving window approach and calculated the observed SRI to be included as a covariate in iSSA models (see section 3.3.2). The first network was calculated for 1 January to 7 January, the second was 2 January to 8 January, and so on. Weekly networks contained 84 relocations per individual (12 relocations per day). For each of these networks I used dyadic values of SRI as a proxy for short-term social preference. I used a three-step process. First, to incorporate SRI within the iSSA framework, I determined the identity and distance (m) of each individual's nearest neighbour at each relocation (Robitaille et al. 2019). Second, for each focal individual and their nearest neighbour at each relocation, I matched the dyadic SRI value for the prior week. For example, for individual A at 12:00 on 8 January, I determined the nearest neighbour was individual B and I extracted the dyadic SRI value for these individuals for the previous week. Third, I repeated steps one and two for all 'available' relocations defined by random steps generated in the iSSA (section 3.3.2). Therefore,

each individual at each relocation had an observed weekly dyadic SRI value and a series of available weekly dyadic SRI values (see section 3.3.2).

In addition to incorporating social preference directly within iSSA models, I also assessed social preference by estimating within-season temporal patterns in associations between individuals by calculating the lagged association rate (LAR). I calculated the LAR within each seasonal proximity-based social network using the *asnipe* package in R (Farine 2013). I calculated LARs within each winter by generating social networks following the procedure described above using GPS relocations. LARs measure the probability that pairs of individuals associating at a given relocation would still associate at subsequent relocations (Whitehead 2008). I compared within-season LARs for individuals in the same annual winter social community to LARs for individuals in different annual winter social communities to assess potential for within-season patterns of association among individuals.

3.3.6 Home range overlap between social communities

To determine spatial overlap of social communities I estimated home ranges during winter using the area of the 95% isopleths from fixed kernel density estimates (Worton 1989) for each social community in each year with the *href* smoothing parameter in the *adehabitatHR* package in R. Data from all individuals in a given social community were pooled to estimate the community home range. I estimated home range overlap between social communities with the utilization distribution overlap index (UDOI), where higher values of UDOI represent a greater proportion of overlap and lower values represent lower proportion of overlap (Fieberg and Kochanny 2005).

3.3.7 Modelling collective movement and habitat selection

We fitted three separate iSSA models for each individual caribou-year (Table S3.1) using the *clogit* function from the *survival* package in R to fit conditional logistic regressions. My first

model was a ‘core model’ (Prokopenko et al. 2017) which tested covariates expected to influence patterns of habitat selection regardless of collective movement. The core model contained four variables: habitat type and interactions between time of day and log-transformed step length and cosine-transformed turn angle. I included the three distinct habitat types in my models: forest, open-foraging, and open-movement. To facilitate model convergence, time of day was a binary category which corresponded to daylight and nighttime hours. Caribou vary their habitat selection and movement throughout the day (Joly 2005). At night, caribou typically rest, while during the day and at twilight, caribou increase movement rates (Maier and White 1998; Joly 2005). Steps were classified as ‘day’ if they fell before sunset and ‘night’ if they fell after sunset. I did not include a twilight category because my inter-fix interval (i.e. two hours) was too long to capture consecutive steps during this time of the day. I used the core model as the foundation on which to add hypothesis-testing covariates.

Our second model included all covariates in the core model as well as nearest neighbour distance. Nearest neighbour distance was calculated for all used and available steps in *spatsoc* (Robitaille et al. 2019). Nearest neighbour distance was log-transformed and included in interactions with turn angle, step length, and habitat type (Table S3.1).

Our third model included all covariates from the core model as well as nearest neighbour distance and weekly dyadic simple ratio index (section 3.3.3). Specifically, I incorporated weekly dyadic SRI values for each observed and available step. Dyadic SRI was included in interactions with turn angle, step length, and habitat type (Table S3.1). Four individuals did not have enough variation in SRI for model convergence and were therefore omitted.

3.4 Results

We found that social associations were stronger among community members, but some individuals associated with members of multiple communities. Depending on the year, social networks comprised 2–6 social communities and although community assortativity (R_{com}) was similar across years, there was high certainty (range = 0.95–1.00) of an individual's assignment to a given community in a given year (Table 3.1). In addition, lagged association rates (LAR) within each winter confirmed temporal stability of community assortment, where association rates for members of the same winter community remained higher than association rates for members of different communities in each year (Figure 3.3). Seasonal winter values of *Q* were significantly lower than the distribution of *Q* generated from null models (Figure S3.1), suggesting that although social networks were structured into communities, inter-community social associations are common (Table 3.1). In support of my expectation of spatial overlap, I observed relatively high spatial overlap between different winter social communities (average UDOI = 0.37, SD = 0.34, range = 0–0.98; Figure S3.2; Table S3.2), thus facilitating the potential for association between social communities.

We found that models including nearest neighbour distance and the simple ratio index were higher ranked compared to the core and nearest neighbour distance models (Table S3.3). For the four individuals that were only included in the core and nearest neighbour distance models, the nearest neighbour distance models were higher ranked (Table S3.3).

We found mixed support for my second set of predictions. In contrast to my expectation, individuals avoided conspecifics while selecting foraging lichen habitat. Specifically, while selecting foraging lichen habitat, 97% (mean coefficient value [β] = 0.464, 95% CI: 0.37, 0.56) of individuals moved further from conspecifics. Although individuals tended to move away from

conspecifics during foraging, 100% (β = 1.02, 95% CI: 0.87, 1.15) of individuals selected nearest neighbours (regardless of distance) that had higher dyadic values of the simple ratio index (Table S3.4; Figure 3.4). These findings suggest that although individuals selected foraging habitat further from conspecifics, they had stronger shared values of the SRI for their nearest neighbours. I also found support for my expectation of collective movement, although there was no effect of social proximity on turning angles. Specifically, 97% (β = 0.17, 95% CI: 0.13, 0.21) of individuals took shorter steps when they were in close proximity to conspecifics, even though 100% (β = 0.48, 95% CI: 0.44, 0.52) of individuals took longer steps when they shared a higher dyadic SRI value with their nearest neighbours (Table S3.4; Figure 3.4). These findings suggest individuals tend to move shorter distances in close proximity to any conspecifics, but further distances when they had stronger shared values of the SRI for their nearest neighbours.

3.5 Discussion

Our study examined apparent social preference in the context of shared space use using socially informed integrated step selection analysis. I present a unified framework that incorporates social networks within a traditional movement ecology and habitat selection framework. Although individual social associations were well mixed at the population level, I found that social networks were structured into discrete communities. Despite spatial overlap between social communities, I highlight two forms of social preference, including long-term temporal stability of associations among individuals as well as an effect of short-term social preference on habitat selection. Further, I found that individual female caribou tended to select foraging habitat spaced away from conspecifics, but moved between foraging habitat with conspecifics, suggesting collective movement is state-dependent. The processes underlying community structure appear to be social, and although it is possible they are spatial, my results indicate there is no spatial

constraint on social associations. Based on my unification of social network analysis with integrated movement and habitat selection analyses, I highlight the influence of collective movement and preferred associations on habitat selection and foraging.

Testing social preference as a driver of movement and habitat selection in my socially informed integrated step selection analysis required establishing the existence of discrete communities and long-term social associations within the population-level network. Indeed, the formation of discrete social communities, in combination with my lagged association analysis, confirm the existence of temporal stability in social associations for members of the same social community. The formation of non-random social communities was driven in part by social preference, but aspects of space use, including shared space, could also influence the stability of social communities (Shizuka et al. 2014). I found high spatial overlap between social communities, suggesting that physical barriers on the landscape do not explain the formation of discrete social communities. For social communities to emerge from a well-mixed population, individuals in different communities must have high spatial, but low temporal overlap in shared geographical space, thus revealing the importance of space and time in the formation of social communities (Cantor et al. 2012). Disentangling space and time within the social environment reveals distinct social communities and groups of individuals that are more likely to associate than by chance (Spiegel et al. 2016). On resource limited landscapes individuals are expected to aggregate in close proximity to resources, for example, elephants (*Loxodonta africana*) aggregate near water-holes (Chamaillé-Jammes et al. 2008). At the population-level, social networks were highly connected, thus providing the impetus to quantify socially informed patterns in movement and habitat selection.

Our findings reveal state-dependent social associations, where individuals selected foraging habitat alone, but moved between foraging patches collectively. Individuals are more likely to trust social information from familiar individuals, but the potential costs are an increase in competition at foraging patches. Individuals may balance the trade-off between competition and access to information by sharing information about the general location of foraging patches in transit but spacing apart at patches to reduce competition. Specifically, when individuals were in closer proximity to one another they selected lichen habitat, which is typically open, allowing them to remain in visual and vocal contact, thereby facilitating social cohesion during foraging despite physically spacing apart (Jacobs 2010). Individuals also took longer steps when they had high social preference for their nearest neighbour. Under the assumption that shorter steps represent foraging behaviour and longer steps represent searching behaviour (Owen-Smith et al. 2010), my results suggest familiar individuals move between foraging patches together. My results reveal potential behavioural mechanisms (i.e. foraging or moving) that influence the frequency and magnitude of social associations.

The emergent geometry of collective movement and spatial arrangement of individuals in a group appears to change as individuals adjust their behaviour based on the availability of resources and the presence of familiar conspecifics (Morrell et al. 2011). Assame macaques (*Macaca assamensis*) distance from one another during foraging, but move collectively between foraging sites (Heesen et al. 2015), while individual giraffes (*Giraffa camelopardalis*) show social preference for conspecifics during foraging, but not during movement (Muller et al. 2018). Interestingly, macaques foraged in closer proximity to individuals of similar dominance rank, while for giraffes it was unclear whether observed social preference was the result of passive or active assortment. For caribou, dominance hierarchies are linear and typically driven by body

size (Barrette and Vandal 1986; Hirotani 1990), suggesting that social preference in caribou could also be related to dominance. My ability to delineate aspects of the social environment between collective movement and habitat selection within a unified framework is useful for disentangling passive or active assortment, for example dominance rank, conspecific attraction, or the transfer of information about foraging resources.

We assumed that solitary foraging is a function of competition among individual caribou for craters in the winter (Barrette and Vandal 1986) and movement in groups could reflect the use of social information about foraging sites (Lesmerises et al. 2018) or predation (Hamilton 1971). Craters can vary in size and distribution (Bergerud 1974); however, craters may only be large enough for a single individual to forage at a time (Mayor et al. 2009). Solitary foraging is therefore most beneficial but foraging in close proximity to preferred conspecifics may be an exception. I propose that while caribou generally have larger group sizes in winter (Jung et al. 2019; Peignier et al. 2019), groups may be sparsely distributed in space to reduce fine-scale competition at individual cratering sites. Groups may spread out such that competition at foraging sites is limited, but group members can retain visual contact. Furthermore, female caribou have antlers, which unlike males, persist into winter. Females are hypothesized to use their antlers to defend craters and exert dominance over both males and females without antlers (Barrette and Vandal 1986; Schaefer and Mahoney 2001). This interpretation is corroborated by theory used to explain fission-fusion dynamics, where individuals are expected to split and merge through space and time to reduce conflict and competition during foraging.

I demonstrate assortment of individuals into distinct social communities, despite high range overlap with individuals in other communities. Integrating space and time revealed fine-scale processes that form social communities and the socially mediated nature of movement

ecology and habitat selection. Within a unified socially-informed integrated step selection framework, I bridge the theoretical and methodological gap between social network analysis (Croft et al. 2011), movement ecology (Nathan et al. 2008), and habitat selection (McLoughlin et al. 2010). I also demonstrate how social association is context dependent, where individuals spaced out during foraging, but moved collectively between foraging patches. My synthesis of integrated step selection analysis and social networks to test hypotheses is an important step towards identifying the roles of physical space and animal space use as factors influencing the social environment (Strandburg-Peshkin et al. 2017). Moreover, individual variation in phenotypes attributable to movement or habitat selection may affect how individuals experience the social environment (Webber and Vander Wal 2018). Movement, habitat selection, and social behaviour are clearly linked; as van Moorter et al. (Van Moorter et al. 2016) described movement as the 'glue' connecting habitat selection to the physical location of a given set of habitats, I posit that movement is the glue connecting individual habitat selection to the social environment.

3.6 Acknowledgements

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Table 3.1: Summary of winter community assignment for three caribou social networks (2017–2019), including the number of individuals (N), number of communities, community size, modularity (Q), and the community assortativity coefficient (R_{com} = 0 indicates no confidence in community assignment; R_{com} = 1 indicates certainty in community assignment).

Year	N	Community	No. Individuals	Home range area (km^2)	*Q*	R_{com}
2017	10	1	3	84.71	0.13	0.95
		2	7	43.43		
2018	16	1	5	113.09	0.17	1.00
		2	7	77.31		
		3	1	13.84		
		4	1	23.11		
		5	1	4.94		
		6	1	19.06		
2019	12	1	2	32.39	0.13	1.00
		2	9	33.87		
		3	1	1.26		

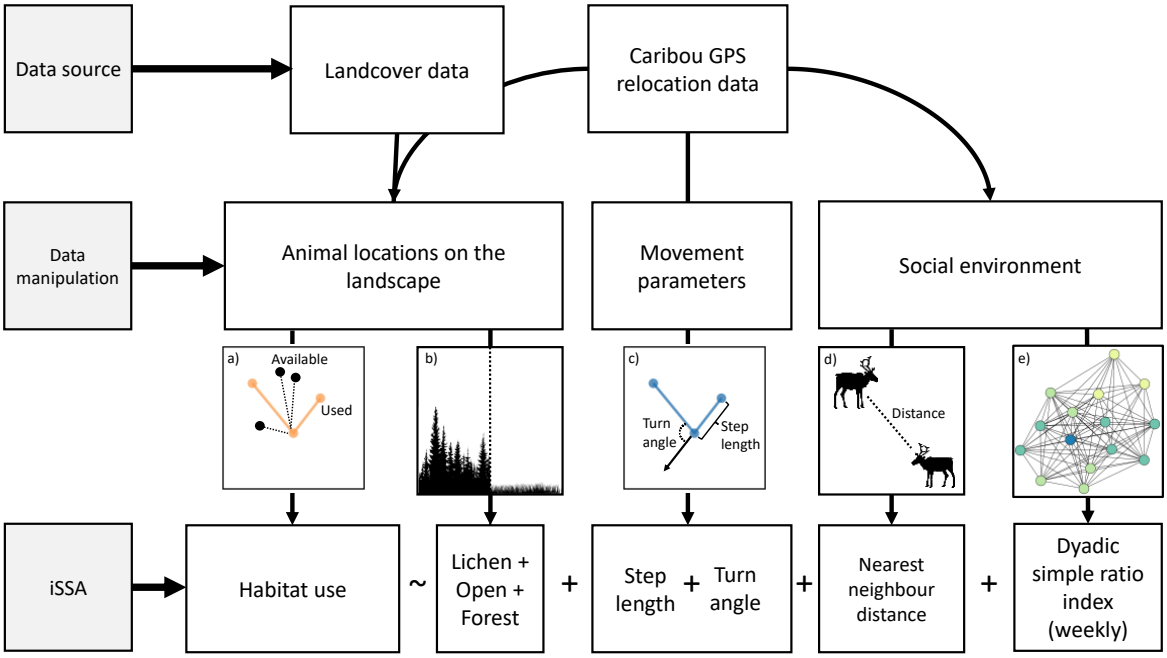

Figure 3.1: Summary of the data pipeline used to generate integrated step selection analysis (iSSA) models. Primary data sources were landcover data and caribou GPS relocation data, which were combined to determine the physical locations of animals on the landscape. The pairing of animal locations and landcover data was used to generate the comparison of used to available points (panel a), which is the response variable in iSSA models, as well as the habitat type in which a given relocation occurred: lichen (defined in text as open-forage), open (defined in text as open-movement), and forest (panel b). Caribou relocation data were also used to generate two movement parameters (panel c) and aspects of the social environment (panels d and e). Movement parameters included turn angle, which is the angular deviation between the headings of two consecutive steps, and step length, which is the linear distance between consecutive relocations (panel c). The social environment included nearest neighbour distance (panel d) and weekly social networks and the dyadic simple ratio index generated based on a moving-window as a proxy for short-term social preference (panel e). The bottom row represents a graphical formulation of my iSSA models, where habitat use (1:10 ratio of used to available

relocations) was regressed against habitat type (lichen, open, and forest), movement parameters (step length and turn angle), nearest neighbour distance, and weekly dyadic simple ratio index.

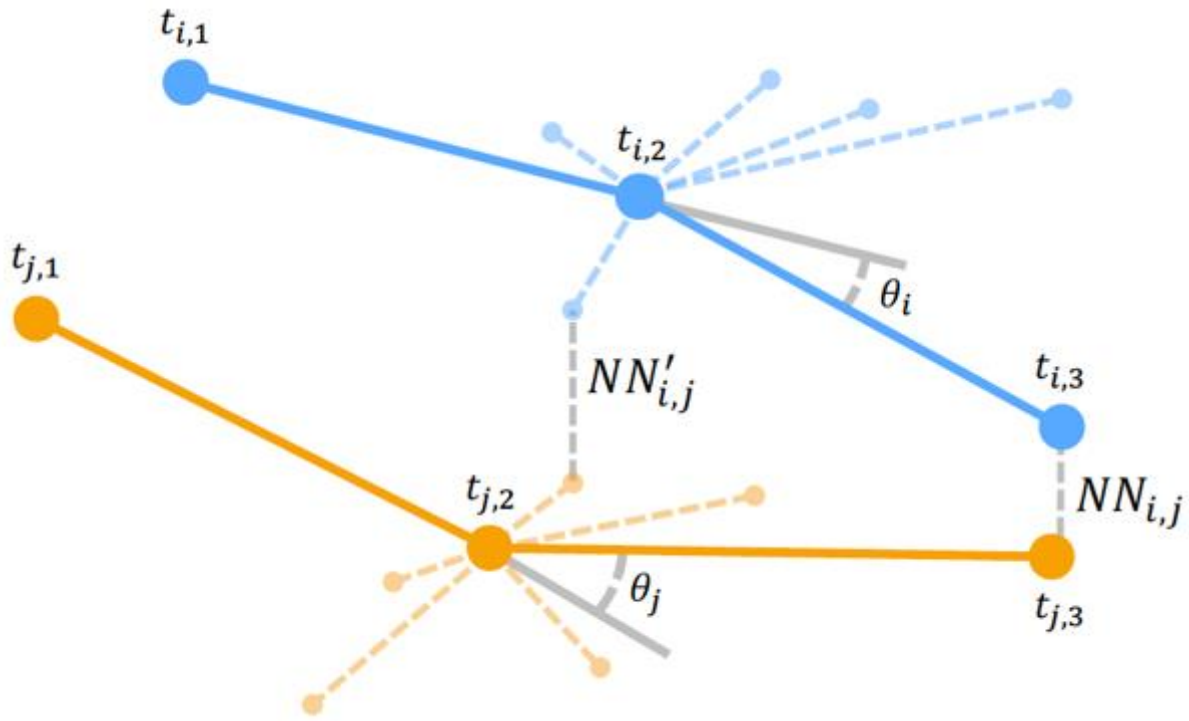

Figure 3.2: Schematic of integrated step selection analysis in the context of social network analysis. Available (random) steps are generated based on the distribution of used step lengths (thin dashed orange and blue lines) and turn angles. I compared used (observed) to available (random) nearest neighbour distance based on fine-scale movement decisions of individuals. Blue lines represent used (dark thick lines) and available (light dashed lines) steps of individual i and orange lines represent used (dark thick lines) and available (light dashed lines) steps of individual *j*. The dashed grey line $(NN_{i,j})$ represents the observed nearest neighbour distance between *i* and *j* at t_3. For each set of available steps, I re-calculated nearest neighbour distance, denoted by a dashed grey line $(NN'_{i,j})$ between available steps for *i* and *j*, which represents the available nearest neighbour distance at a given iteration. Step length is the distance between the used start (e.g. $t_{j,2}$) point and the step end point ($t_{j,3}$) and turn angle is calculated as the angular deviation between the previous step heading (grey line and θ_i and θ_j) and the subsequent used step.

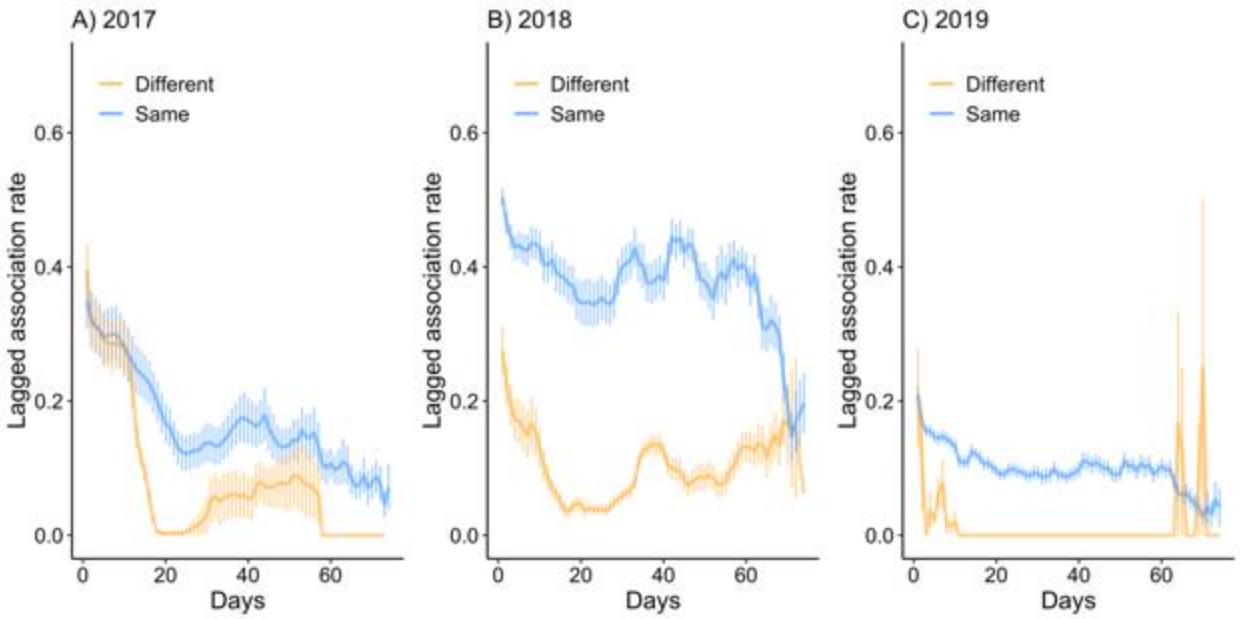

Figure 3.3: Observed lagged association rate (LAR) for caribou in the same (blue lines) and different (orange) annual winter social communities, calculated as the probability that any pair of individuals associated on a given day, are still associated on subsequent days. Note, the time period for LAR analysis and social community assignment was 1 January to 16 March. Error bars represent the standard error of all pairwise association rates calculated on each day. Individuals in the same social communities (blue lines) generally had higher lagged association rates, suggesting they were more likely to associate together over time.

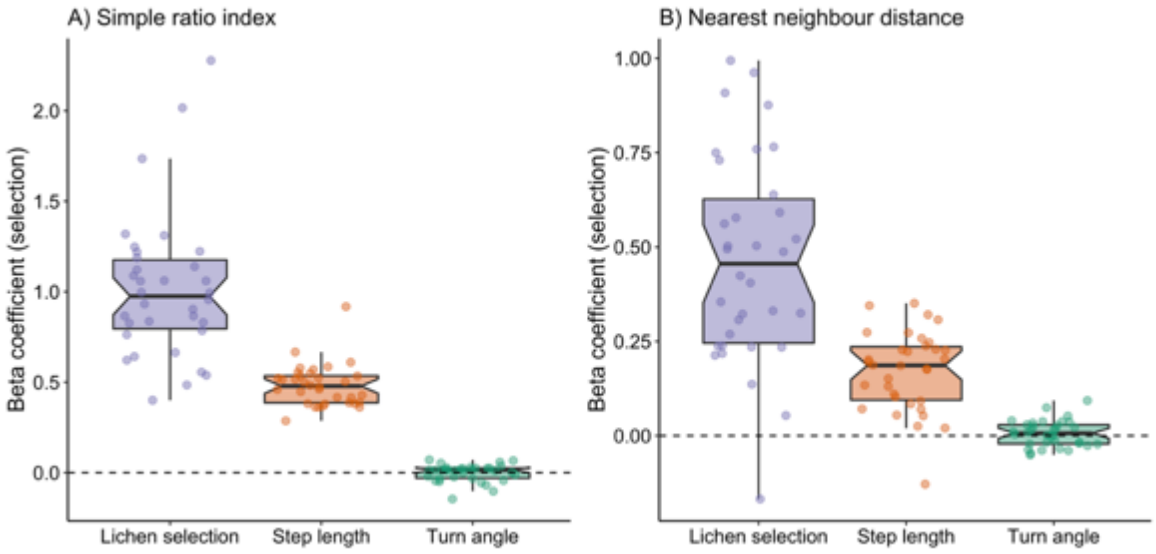

Figure 3.4: Individual habitat selection coefficients for interactions between A) short-term dyadic simple ratio index (SRI) and each of lichen selection, step length, and turn angle; B) interactions between nearest neighbour distance and each of lichen selection, step length, and turn angle. Individuals selected lichen habitat when they had a higher shared SRI value with their nearest neighbour (Panel A, purple box) and when they are further from neighbours (Panel B, purple box). Individuals took longer steps when they had a higher shared SRI value with their nearest neighbour (Panel A, orange box) and when their nearest neighbours are further (Panel B, orange box). Interactions between turn angle and shared SRI values (Panel A, green box) and nearest neighbour distance (Panel B, green box) were not significant. Positive coefficients for interactions with SRI (Panel A) indicate selection for nearest neighbours with a higher shared SRI value, while negative coefficients for interactions with SRI indicate selection for nearest neighbours with a lower shared SRI value; positive coefficients for interactions with nearest neighbour distance (Panel B) indicates selection for greater distance and negative coefficients for interactions with nearest neighbour distance indicates selection for shorter distance from conspecifics. Horizontal dashed line denotes zero, the point where coefficients represent neither

selection or avoidance of a given habitat or behaviour. Points show the distribution of data, thick dark lines represent the median, upper and lower edges of each box represent the interquartile range (25% and 75% of data), notches represent the difference in median in each season, and whiskers represent the upper and lower quantiles (2.5% and 97.5% of data).

3.7 References

Avgar T, Potts JR, Lewis MA, Boyce MS. 2016. Integrated step selection analysis: Bridging the gap between resource selection and animal movement. Methods Ecol Evol. 7(5):619–630. doi:10.1111/2041-210X.12528.

Barrette C, Vandal D. 1986. Social rank, dominance, antler size, and access to food in snow-bound wild woodland caribou. Behaviour. 97(1):118–145.

van Beest FM, Uzal A, Vander Wal E, Laforge MP, Contasti AL, Colville D, Mcloughlin PD. 2014. Increasing density leads to generalization in both coarse-grained habitat selection and fine-grained resource selection in a large mammal. J Anim Ecol. 83(1):147–156. doi:10.1111/1365-2656.12115.

Bergerud AT. 1974. Relative abundance of food in winter for Newfoundland caribou. Oikos. 25(3):379–387.

Bergerud AT, Mercer WE. 1989. Caribou introductions in eastern North America. Wildl Soc Bull. 17(2):111–120.

Best EC, Seddon JM, Dwyer RG, Goldizen AW. 2013. Social preference influences female community structure in a population of wild eastern grey kangaroos. Anim Behav. 86(5):1031–1040. doi:10.1016/j.anbehav.2013.09.008.

Bjørneraas K, Van Moorter B, Rolandsen CM, Herfindal I. 2010. Screening Global Positioning System Location Data for Errors Using Animal Movement Characteristics. J Wildl Manage. 74(6):1361–1366. doi:10.2193/2009-405.

Boertje RD. 1985. An Energy Model for Adult Female Caribou of the Denali Herd, Alaska. J Range Manag. 38(5):468–473. doi:10.2307/3899725.

Cairns SJ, Schwager SJ. 1987. A comparison of association indices. Anim Behav. 35:1454–1469.

Cantor M, Wedekin LL, Guimarães PR, Daura-Jorge FG, Rossi-Santos MR, Simões-Lopes PC. 2012. Disentangling social networks from spatiotemporal dynamics: The temporal structure of a dolphin society. Anim Behav. 84(3):641–651. doi:10.1016/j.anbehav.2012.06.019.

Chamaillé-Jammes S, Fritz H, Valeix M, Murindagomo F, Clobert J. 2008. Resource variability, aggregation and direct density dependence in an open context: The local regulation of an African elephant population. J Anim Ecol. 77(1):135–144. doi:10.1111/j.1365-2656.2007.01307.x.

Creel S, Schuette P, Christianson D. 2014. Effects of predation risk on group size, vigilance, and foraging behavior in an African ungulate community. Behav Ecol. 25(4):773–784. doi:10.1093/beheco/aru050.

Croft DP, Darden SK, Wey TW. 2016. Current directions in animal social networks. Curr Opin Behav Sci. 12:52–58. doi:10.1016/j.cobeha.2016.09.001.

Croft DP, Madden JR, Franks DW, James R. 2011. Hypothesis testing in animal social networks. Trends Ecol Evol. 26(10):502–507. doi:10.1016/j.tree.2011.05.012.

Csárdi G, Nepusz T. 2006. The igraph software package for complex network research. InterJournal Complex Syst. 1695:1–9.

Duchesne T, Fortin D, Rivest LP. 2015. Equivalence between step selection functions and biased correlated random walks for statistical inference on animal movement. PLoS One. 10(4):1–12. doi:10.1371/journal.pone.0122947.

Duquette LS, Klein DR. 1987. Activity budgets and group size of caribou during spring migration. Can Jounal Zool. 65(164–168).

Farine DR. 2013. Animal social network inference and permutations for ecologists in R using asnipe. Methods Ecol Evol. 4(12):1187–1194. doi:10.1111/2041-210X.12121.

Farine DR. 2014. Measuring phenotypic assortment in animal social networks: Weighted associations are more robust than binary edges. Anim Behav. 89:141–153. doi:10.1016/j.anbehav.2014.01.001.

Farine DR, Whitehead H. 2015. Constructing, conducting and interpreting animal social network analysis. J Anim Ecol. 84:1144–1163. doi:10.1111/1365-2656.12418.

Fieberg J, Kochanny CO. 2005. Quanitfying home-range overlap: the importance of the utilization distribution. J Wildl Manage. 69(4):1346–1359. doi:10.2193/0022-541X(2005)69.

Fortin D, Beyer HL, Boyce MS, Smith DW, Duchesne T, Mao JS. 2005. Wolves influence elk movements: Behavior shapes a trophic cascade in Yellowstone National Park. Ecology. 86(5):1320–1330.

Fortin D, Courtois R, Etcheverry P, Dussault C, Gingras A. 2008. Winter selection of landscapes by woodland caribou: Behavioural response to geographical gradients in habitat attributes. J Appl Ecol. 45(5):1392–1400. doi:10.1111/j.1365-2664.2008.01542.x.

Giraldeau L-A, Caraco T. 2018. Social foraging theory. Princeton University Press.

Giraldeau LA, Dubois F. 2008. Social foraging and the study of exploitative behavior. Adv Study Behav. 38(08):59–104. doi:10.1016/S0065-3454(08)00002-8.

Hamilton WD. 1971. Geometry for the selfish herd. J Theor Biol. 31(2):295–311. doi:10.1016/0022-5193(71)90189-5.

Harel R, Spiegel O, Getz WM, Nathan R. 2017. Social foraging and individual consistency in

following behaviour: testing the information centre hypothesis in free-ranging vultures. Proc R Soc B. 284:20162654.

He P, Maldonado-Chaparro AA, Farine DR. 2019. The role of habitat configuration in shaping social structure: a gap in studies of animal social complexity. Behav Ecol Sociobiol. 73:9.

Heesen M, Macdonald S, Ostner J, Schülke O. 2015. Ecological and Social determinants of group cohesiveness and within-group spatial position in wild assamese macaques. Ethology. 121(3):270–283. doi:10.1111/eth.12336.

Hirotani A. 1990. Social organization of reindeer (*Rangifer tarandus*), with a special reference to relationships among females. Can J Zool. 68(4):743–749.

Jacobs A. 2010. Group cohesiveness during collective movements: Travelling apart together. Behav Processes. 84(3):678–680. doi:10.1016/j.beproc.2010.03.004.

Jolles JW, King AJ, Killen SS. 2019. The role of individual heterogeneity in collective animal behaviour. Trends Ecol Evol. 35:278–291. doi:10.1016/j.tree.2019.11.001.

Joly K. 2005. The effects of sampling regime on the analysis of movements of overwintering female caribou in east-central Alaska. Rangifer. 25(2):67–74. doi:10.7557/2.25.2.254.

Jones TB, Patrick SC, Evans JC, Wells MR. 2020. Consistent sociality but flexible social associations across temporal and spatial foraging contexts in a colonial breeder. Ecol Lett. 23:1085–1096. doi:10.1111/ele.13507.

Jung TS, Larter NC, Allaire DG. 2019. Social organization of boreal woodland caribou (*Rangifer tarandus caribou*) in response to decreasing annual snow depth. Mammal Res. 64:377–385.

Kasozi H, Montgomery RA. 2020. Variability in the estimation of ungulate group sizes complicates ecological inference. Ecol Evol.(May):1–9. doi:10.1002/ece3.6463.

Lachlan RF, Crooks L, Laland KN. 1998. Who follows whom? Shoaling preferences and social learning of foraging information in guppies. Anim Behav. 56(1):181–190. doi:10.1006/anbe.1998.0760.

Lesmerises F, Johnson CJ, St-Laurent M-H. 2018. Landscape knowledge is an important driver of the fission dynamics of an alpine ungulate. Anim Behav. 140:39–47. doi:10.1016/j.anbehav.2018.03.014.

Lewis KP. 2014. Sustainable Development and Strategic Science Branch Land Cover Classification.

Lima SL. 1995. Back to the basics of anti-predatory vigilance: the group-size effect. Anim Behav. 49:11–20.

Maier J, White R. 1998. Timing and synchrony of activity in caribou. Can Jounal Zool. 76(22):1999–2009.

Mayor SJ, Schaefer JA, Schneider DC, Mahoney SP. 2009. The spatial structure of habitat selection: A caribou's-eye-view. Acta Oecologica. 35(2):253–260. doi:10.1016/j.actao.2008.11.004.

McLoughlin PD, Morris DW, Fortin D, Vander Wal E, Contasti AL. 2010. Considering ecological dynamics in resource selection functions. J Anim Ecol. 79(1):4–12. doi:10.1111/j.1365-2656.2009.01613.x.

Van Moorter B, Rolandsen CM, Basille M, Gaillard J-M. 2016. Movement is the glue connecting home ranges and habitat selection. J Anim Ecol. 85:21–31. doi:10.1111/1365-2656.12394.

Morrell LJ, Ruxton GD, James R. 2011. Spatial positioning in the selfish herd. Behav Ecol. 22(1):16–22. doi:10.1093/beheco/arq157.

Mourier J, Vercelloni J, Planes S. 2012. Evidence of social communities in a spatially structured network of a free-ranging shark species. Anim Behav. 83(2):389–401. doi:10.1016/j.anbehav.2011.11.008.

Muller Z, Cantor M, Cuthill IC, Harris S. 2018. Giraffe social preferences are context dependent. Anim Behav. 146:37–49. doi:10.1016/j.anbehav.2018.10.006.

Nathan R, Getz WM, Revilla E, Holyoak M, Kadmon R, Saltz D, Smouse PE. 2008. A movement ecology paradigm for unifying organismal movement research. Proc Natl Acad Sci. 105(49):19052–19059. doi:10.1073/pnas.0800375105.

Newman MEJ. 2006. Modularity and community structure in networks. Proc Natl Acad Sci. 103(23):8577–8582.

Owen-Smith N, Fryxell JM, Merrill EH. 2010. Foraging theory upscaled: the behavioural ecology of herbivore movement. Philos Trans R Soc B. 365(1550):2267–2278. doi:10.1098/rstb.2010.0095.

Patin R, Fortin D, Sueur C, Chamaillé-Jammes S. 2019. Space use and leadership modify dilution effects on pptimal vigilance under food-safety trade-offs. Am Nat. 193(1):E15–E28. doi:10.1086/700566.

Peignier M, Webber QMR, Koen EL, Laforge MP, Robitaille AL, Vander Wal E. 2019. Space use and social association in a gregarious ungulate: Testing the conspecific attraction and resource dispersion hypotheses. Ecol Evol. 9:5133–5145. doi:10.1002/ece3.5071.

Pinter-Wollman N, Hobson EA, Smith JE, Edelman AJ, Shizuka D, De Silva S, Waters JS, Prager SD, Sasaki T, Wittemyer G, et al. 2013. The dynamics of animal social networks:

Analytical, conceptual, and theoretical advances. Behav Ecol. 25(2):242–255. doi:10.1093/beheco/art047.

Prokopenko CM, Boyce MS, Avgar T. 2017. Characterizing wildlife behavioural responses to roads using integrated step selection analysis. J Appl Ecol. 54:470–479. doi:10.1111/1365-2664.12768.

R Core Team. 2019. R: A language and environment for statistical computing. :https://www.r-project.org/.

Robitaille AL, Webber QMR, Vander Wal E. 2019. Conducting social network analysis with animal telemetry data: applications and methods using spatsoc. Methods Ecol Evol. 10:1203–1211. doi:10.1111/2041-210X.13215.

Schaefer JA, Mahoney SP. 2001. Antlers on female caribou: Biogeography of the bones of contention. Ecology. 82(12):3556–3560.

Shizuka D, Chaine AS, Anderson J, Johnson O, Laursen IM, Lyon BE. 2014. Across-year social stability shapes network structure in wintering migrant sparrows. Ecol Lett. 17(8):998–1007. doi:10.1111/ele.12304.

Shizuka D, Farine DR. 2016. Measuring the robustness of network community structure using assortativity. Anim Behav. 112:237–246.

Signer J, Fieberg J, Avgar T. 2019. Animal movement tools (amt): R package for managing tracking data and conducting habitat selection analyses. Ecol Evol. 9(July 2018):880–890. doi:10.1002/ece3.4823.

Silk JB. 2007. Social components of fitness in primate groups. Science (80-). 317(5843):1347–1351.

Spiegel O, Crofoot MC. 2016. The feedback between where we go and what we know—information shapes movement, but movement also impacts information acquisition. Curr Opin Behav Sci. 12:90–96. doi:10.1016/j.cobeha.2016.09.009.

Spiegel O, Leu ST, Bull CM, Sih A. 2017. What's your move? Movement as a link between personality and spatial dynamics in animal populations. Ecol Lett. 20(1):3–18. doi:10.1111/ele.12708.

Spiegel O, Leu ST, Sih A, Bull CM. 2016. Socially interacting or indifferent neighbours? Randomization of movement paths to tease apart social preference and spatial constraints. Methods Ecol Evol. 7:971–979. doi:10.1111/2041-210X.12553.

Spiegel O, Sih A, Leu ST, Bull CM. 2018. Where should we meet? Mapping social network interactions of sleepy lizards shows sex-dependent social network structure. Anim Behav. 136:207–215. doi:10.1016/j.anbehav.2017.11.001.

Strandburg-Peshkin A, Farine DR, Crofoot MC, Couzin ID. 2017. Habitat structure shapes individual decisions and emergent group structure in collectively moving wild baboons. Elife. 6:e19505. doi:10.7554/eLife.19505.

Strandburg-Peshkin A, Papageorgiou D, Crofoot MC, Farine DR. 2018. Inferring influence and leadership in moving animal groups. Philos Trans R Soc B. 373:20170006. doi:10.1098/not.

Webber QMR, Vander Wal E. 2018. An evolutionary framework outlining the integration of individual social and spatial ecology. J Anim Ecol. 87:113–127. doi:10.1111/1365-2656.12773.

Whitehead H. 2008. Analyzing animal societies: quantitative methods for vertebrate social analysis. University of Chicago Press.

Worton BJ. 1989. Kernel methods for estimating the utilization distribution in home-range studies. Ecology. 70(1):164–168.

CHAPTER 4: POST-RUT AGGRESSION IN CARIBOU: LIMITED EVIDENCE FOR INTERFERENCE COMPETITION BUT STRONG EVIDENCE FOR MALE HARASSMENT

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4.1 Abstract

Social competition for resources is widespread among animals. Females of many species compete for foraging resources through interference competition, which is a behavioural interaction between animals that reduces an individual's access to shared resources. In addition to competition from other females, females also often face harassment from males during and after the breeding season. The female competition hypothesis predicts that female-initiated aggression associated with foraging competition increases as a function of group size, but I expected this effect to be more pronounced in higher quality foraging habitat. The male harassment hypothesis predicts that male harassment of females should also increase as a function of group size as well as a function of the ratio of males to other group members. Here, I tested the female competition and male harassment hypotheses for caribou (*Rangifer tarandus*) within the context of variation in the social environment (i.e. group size and sex ratio) and the physical environment (i.e. variation in habitat quality). I conducted focal observations of caribou on Fogo Island, Newfoundland, groups over three years and quantified aggressive social interactions in different habitat types to test my hypotheses. Specifically, I took advantage of natural variation in caribou behaviour in my system and observed caribou foraging in an enhanced habitat (i.e. recreational sports complex field) and natural habitat (i.e. lichen barrens). I found limited support for the female competition hypothesis, possibly as a result of females' propensity to increase foraging rates in enhanced habitats. By contrast, I found strong support for the male harassment hypothesis, where males increase the frequency of harassment as group size increased. Together, my results suggest that females in the Fogo Island caribou herd may balance the costs of group living to reduce the potential somatic costs associated with male harassment, but not competition from other females.

4.2 Introduction

Social competition for resources, including food and mates, is widespread among animals (West-Eberhard 1979). Within studies of social behaviour, competition is often cited as a cost to sociality. In birds, competition for food can be intense and occasionally involves fighting over available resources (Goss-Custard 1980), while in mammals, competition can also resort in fighting, but fighting is sex specific (Clutton-Brock and Huchard 2013b). In contrast to males, female competition in mammals typically does not involve fighting contests associated with exaggerated secondary sexual characteristics (Clutton-Brock and Huchard 2013a, b). In many mammals specifically, competition among females tends to relate to food acquisition and maintenance of social rank and includes aggressive interactions, fighting, and resource defence (Clutton-Brock and Huchard 2013a). As a result, competition among females can disrupt foraging activities, thereby inducing somatic costs (Tennenhouse et al. 2011). Females also suffer somatic costs due to male harassment during, and after the breeding season (Holand et al. 2006; Uccheddu et al. 2015). For species with polygynous mating system, smaller and younger males tend to be excluded from mating opportunities during the breeding season and these individuals attempt mating after the breeding season (Holand et al. 2006; Airst and Lingle 2019). The extent to which females compete with each other and suffer harassment from males can be driven by aspects of the physical environment (e.g., the distribution and availability of food) and the social environment (e.g. the size, composition, and cohesiveness of social groups) (Uccheddu et al. 2015; Stutz et al. 2018). When high quality foraging patches are heterogeneously distributed, animals tend to aggregate at these sites, and competition among females is expected to intensify (Chamaillé-Jammes et al. 2008). When males and females aggregate in groups, the potential for male harassment of females is also expected to intensify (Uccheddu et al. 2015).

The social and physical environments are therefore two axes of variation that can influence fine-scale social interactions, including aggression or fighting (Webber and Vander Wal 2018). Here, I examine how competition between females and male harassment of females vary as a function of the physical, i.e. food availability, and social environments, i.e. group size and composition.

Interference competition is a common type of competition and is a behavioural interaction between animals that reduces an individual's access to shared resources (Cresswell 1998; Folmer et al. 2012). For example, interference competition in male and female blackbirds (*Turdus merula*) includes chasing behaviour and varies depending on the density of prey (Cresswell 1998). Although the per capita rate of vigilance decreases with increasing group size (Lima 1995), interference competition is predicted to increase as a function of group size and interference may also manifest as lost foraging opportunities due to an increase in intra-specific vigilance or avoidance behaviour directed toward conspecifics (Sansom et al. 2008). Furthermore, within the context of the physical environment, concentrated resources can lead to animals aggregating at these resources and increasing interference competition (Hirsch 2007). Concentrated, higher quality foraging patches are therefore predicted to result in heightened aggression through interference competition (Hall 1983; Veiberg et al. 2004), and the social and physical environments can both affect variation in competition.

Aggression, which can include non-contact signalling as well as physical contact and fighting, is an important form of social interaction that is often associated with competition. Aggression can be adaptive in the context of resource and territory defense (Cassidy et al. 2015; Siracusa et al. 2017), mate competition (Clutton-Brock et al. 1979), and foraging (Peterson and Weckerly 2018). The type and intensity of aggression in mammals can also be sex-specific with females typically displaying lower overall levels (Clutton-Brock and Huchard 2013b). For

example, females are more likely to engage in displays of dominance or other non-physical contests than males (but for exceptions see Clutton-Brock and Huchard 2013b). For social species that do not defend territories, aggression among females is most likely to manifest as interference competition during foraging (Uccheddu et al. 2015). Specifically, when habitat quality varies spatially, aggregation at concentrated, high quality foraging sites could elicit particularly high rates of aggression and interference competition (Weckerly et al. 2014). In addition to competition among females, male harassment can also disrupt female foraging activities (Tobler et al. 2011). For ungulates, male harassment typically increases during the breeding season, but it can also continue after peak breeding. Specifically, males investigate and harass females to ascertain whether females are in oestrus (Clutton-Brock et al. 1992; Isvaran 2005). In addition, younger males are also known to harass females as a form of socialization and possibly to adopt sneaking mating tactics after the peak breeding season has ended (Weladji et al. 2017). Female foraging can therefore be disrupted by interference competition from other females *and* harassment from males. Interference competition during foraging is predicted to intensify as group size increases and spacing between individuals decreases (Fournier and Festa-Bianchet 1995), and male harassment is predicted to increase as the male sex ratio in a group increases (Uccheddu et al. 2015).

Caribou and reindeer (*Rangifer tarandus*) are gregarious ungulates that live in fission-fusion societies (Lesmerises et al. 2018b) with linear dominance hierarchies among females organized by body size and the presence of antlers (Barrette and Vandal 1986; Hirotani 1990). When female caribou are aggressive towards other females, it is often related to foraging opportunities, while male aggression towards females tends to be related to harassment during and after the rutting period (Uccheddu et al. 2015). I observed free-ranging groups of caribou in

two distinct foraging contexts: groups foraging in either natural habitats (i.e. lichen barrens), or enhanced habitats (i.e. grass at a recreational sports field; see Methods for details) to test the female forage competition and male harassment hypotheses. I considered natural habitats to be lower quality compared to enhanced habitat. I specifically tested predictions about the role of the social and physical environments, including group size and composition and the quality of foraging patches, as drivers of intra-specific vigilance, sex-specific aggression, among-female competition, and male harassment in caribou. Specifically, I examined ten predictions:

1) The interference competition hypothesis predicts that as group size increases, the frequency of intra-specific vigilance should increase (P1a). I also predicted that, regardless of group size, the proportion individuals foraging would be higher in higher quality foraging habitats (P1b).
2) We predicted that the frequency of female-initiated aggression would increase as a function of group size because interference competition among females is expected to increase as group size increases (P2a). I also predicted the effect of group size on female-initiated aggression would be greater in artificially enhanced foraging habitats compared to natural habitats because competition for foraging opportunities in enhanced habitats is assumed to be more intense than in natural habitats (P2b).
3) We predicted the frequency of male-initiated aggression would be higher than female-initiated aggression (P3a) and that female-initiated aggression would be greater in enhanced foraging habitats compared to natural habitats (P3b). I also predicted that female-initiated aggression would be predominantly non-contact interactions, while male-initiated aggression would be predominantly contact interactions (P3c).

4) We predicted that the frequency of male harassment would increase as a function of group size (P4a) and adult sex ratio of the group (P4b) as a result of increased competition among males as the number of males increased. I also predicted that male harassment would be greater in artificially enhanced foraging habitats compared to natural habitats (P4c).

4.3 Methods

4.3.1 Study area and caribou natural history

Fogo Island is a small island off the northeast coast of the Island of Newfoundland, Canada. Newfoundland, and Fogo Island, have a humid-continental climate and persistent precipitation throughout the year. Between 1964-1967, 26 caribou were introduced to Fogo Island from the island of Newfoundland as part of a series of introductions and translocations (Bergerud and Mercer 1989). The Fogo Island herd increased in size from 26 individuals in the 1960s to ~300 at present; over the last ten years, population density has remained stable (Newfoundland and Labrador Wildlife Division total counts, unpublished data). The only predator of caribou on Fogo Island is coyote (*Canis latrans*). In Newfoundland, coyotes primarily predate caribou calves (Rayl et al. 2014), although they also occasionally predate adults (Lewis and Mahoney 2014). Caribou habitat on Fogo Island consists of black spruce (*Picea mariana*), balsam fir (*Abies balsamea*), and white birch (*Betula papyrifera*) interspersed with bogs, lakes, and barren rock. Within their range in Newfoundland, caribou forage primarily on lichen, grasses, sedges, and other deciduous browse in summer and almost exclusively lichen in winter (Bergerud 1974a; Mahoney and Virgl 2003; Schaefer et al. 2016).

Caribou groups vary in size throughout the year (Lesmerises et al. 2018b). Groups are typically largest in winter and shortly after calving and smallest in summer (Chapter 5), while

caribou typically form small to medium sized groups during the rut (Bergerud 1974b). Caribou and reindeer form loose harems where dominant males defend a small number of females against subordinate males (Body et al. 2014). In Newfoundland, the rut typically occurs in early to mid-October and by November, the majority of harem groups have disbanded (Bergerud 1974b). The post-rutting period therefore represents a transition between the rut and winter seasons, which tend to have distinct social grouping patterns.

4.3.2 Data collection in the field

We observed groups of caribou in 2017 (25–27 November), 2018 (2–12 November), and 2019 (4–22 November). I located groups of caribou either by tracking radio-collared females (Peignier et al. 2019) or by opportunistically discovering groups. Groups of caribou were located in one of two broad contexts, either in natural habitats or enhanced habitats. I deemed foraging opportunities at the recreational sports complex field were higher quality than surrounding lichen barrens for two reasons: 1) this area was fertilized throughout the summer; and 2) during data collection in November, the grass remained green compared to surrounding vegetation, which was brown or yellow (see Figure S4.1 for visual comparison).

To assign groups, I applied the "chain rule" when determining group size and assumed that two or more individuals were in the same group if they were within ~50 m of at least one other individual based on visual observation (Kasozi and Montgomery 2020). Upon encountering a group, I determined the size and composition of the group and began video recording the group for subsequent behavioural analysis. All video recordings occurred between 0800 and 1400 h. I only recorded groups of at least three individuals (observed groups ranged in size from 3–63; Figure S4.2), and recordings lasted for at least five minutes (average ± standard deviation = 17 ± 4 min, range = 7–26 min). I was typically anywhere from 50–500 m from caribou during focal

observations and I terminated recording sessions if caribou moved out of view or if my presence was detected by caribou in the field and caribou either changed their behaviour or left the area. Because caribou live in fission-fusion societies and the majority of individuals in the population are unmarked, it was not possible to record a measure of group identity from day to day. However, in some cases I was able to follow a single group and recorded multiple videos of the same group on the same day. I therefore assigned a unique group identifier, but different video identifiers, to all groups to account for a potential confound in statistical analyses (see below). In total, I conducted 41 group observations totaling 740 minutes (12 hours and 26 minutes) and observed 848 social interactions.

4.3.3 Measuring behaviour

I quantified behaviour of caribou groups using two techniques: instantaneous group scans and focal observation of aggressive interactions. I performed instantaneous group scan sampling of the group every minute and recorded the number of caribou per group engaged in one of four behaviours: feeding, standing, moving, or laying down. Feeding is typically separated into eating and searching (Witter et al. 2012). I grouped these behaviours together because they were difficult to disentangle at a distance. Feeding was therefore defined as any instance where the caribou had their muzzle to the ground and was either ingesting vegetation or investigating the ground surface, but not ingesting vegetation. Standing was defined as a caribou that was stationary with their head raised, moving was defined as a caribou walking or running with their head raised (as opposed to their head down feeding, see above), and laying down was defined as a caribou with all four legs on the ground, but their head could be raised or lowered. As a result of recording caribou behaviour during foraging, continuous moving was relatively rare, so I grouped standing and moving for subsequent analyses. For each scan sampling event, I recorded

the number of caribou visible in the video frame. In cases when caribou either left the frame of the video or were obstructed by other objects in the field, I did not include them in the scan. I was unable to track specific individuals throughout a single video, so analyses based on the scan and occurrence sampling were anonymous to the identity of individuals.

We performed all occurrence sampling of aggressive behaviours by recording behaviours as they occurred. I categorized the type of aggression as one of six behaviours: displacement, sparring, head butt, kicking, rearing, and male harassment of females (see Table 4.1 for definitions). For displacement, head butt, kicking, and rearing I noted whether there was physical contact between the individuals, and categories of sparring were delineated based on the duration of time two individuals spent sparring. I recorded the frequency of aggressive behaviours and, if possible, I recorded the sex (male or female) of the initiator and recipient of each behaviour. Overall, I recorded the sex of the initiator for 77% of interactions (653/848) and for subsequent analyses where sex was a predictor for aggression (P2, P3, and P4) I excluded interactions where I was unable to identify the sex of the initiator. I also excluded interactions where a male was the initiator and the recipient of the interaction, as this was not the focus of my analysis.

4.3.4 Statistical analysis

All analyses were conducted in R (R Core Team 2019). To test my hypotheses, I conducted five sets of models using the *glmmTMB* R package (Brooks et al. 2017). For the first two model sets, I used beta regression to model the average proportion of individuals vigilant and the average proportion of individuals foraging during a focal scan. First, I modelled the average proportion of individuals that were vigilant in a scan observation, calculated as the total number of animals vigilant divided by the total number of individuals visible within the video frame. Second, I modelled the average proportion of individuals that were foraging or searching for forage in a

scan observation, calculated as the total number of animals foraging or searching for forage divided by the total number of individuals visible within the video frame. I calculated the proportion of animals vigilant or foraging for each video observation (n = 41). Beta regression is commonly used to model proportional data that are bounded between 0 and 1 (Douma and Weedon 2019). Due to the relatively low frequency of lying down (see above), I omitted this variable from analyses. For both models, I included group size and habitat type (enhanced or natural) as fixed effect covariates (P1a and P1b). I also included year of study (2017, 2018, or 2019) and group identity as random effects.

For the next three sets of models (P2-P4), I used the frequency of interactions (either aggression or harassment) in each video observation as the response variable in each model. Count data are often right-skewed, so I parameterized each of the following models with Poisson distribution and negative binomial error structures in the *glmmTMB* R package (Brooks et al. 2017). To ensure appropriate model fit, I compared models with different distributions using AIC model selection to determine which error structure best fit the data. For each video observations, I calculated the frequency of aggressive interactions in different contexts, depending on the predictions.

Specifically, to test my second (P2a and P2b) and third (P3a, P3b, and P3c) sets of predictions I fit a single model where the frequency of aggressive interactions was the response variable in a general linear mixed model with the duration of the video, group size, sex of the initiating individual (male or female), behaviour (contact or non-contact), habitat type (enhanced or natural), and year (2017, 2018, or 2019) as well as interactions between group size and habitat type, habitat and sex, and behaviour and sex as fixed effects. As a result of including the frequency of contact and non-contact aggressive interactions for each video observation period,

there were two measures per video, so I included video identity and group identity as random effects. The top model for this model set was fit with a Poission distribution (Table S4.1).

Finally, to test my fourth set of predictions (P4a, P4b, and P4c), I fit the frequency of male harassment interactions towards females as the response variable in a linear model with group size, sex ratio, and habitat type (enhanced or natural) and interactions between group size and habitat and sex ratio and habitat as covariates. For this model, I only included one value per video observation, I only included group identity as a random effect. The top model for this model set was fit with a negative binomial distribution (Table S4.1).

4.4 Results

We observed a total of 848 aggressive interactions between caribou over three years (n = 647 enhanced habitat; n = 201 natural habitat). Although the majority of aggression interactions were observed in enhanced (76.3%, 647/848) compared to natural habitats (23.7%, 201/848), the trends I observed were similar between habitat types (Figure 4.1). Specifically, displacement behaviour was the most common type of interaction in both habitat types (39.7%, 337/848), while male harassment (19.8%, 168/848) and sparring (18.6%, 158/848) were the second and third most common behaviours, respectively (Figure 4.1). Head butting (12.7%, 108/848), rearing (5.19%, 44/848), and kicking (3.89%, 33/848) were the least common behaviours (Figure 4.1). Group sizes, as well as the number of males and females, were similar between enhanced and natural habitats (Figure S4.2).

4.4.1 Interference competition hypothesis

We found no effect of group size on the proportion of time spent vigilant or time spent foraging (P1a), however, I found the proportion of time spent foraging was higher in enhanced habitats (P1b, Figure 4.2; Table 4.2). Further, I did not find support for my second set of predictions

associated with the interference competition hypothesis (P2a and P2b). In contrast to P2, there was no effect of group size (P2a), or the interaction between group size and habitat type (P2b), on the rate of female-initiated aggression (Figure 4.3; Table 4.3). I found partial support of my predictions associated with sex-specific aggression (P3a and P3b). Specifically, I found that the frequency of male-initiated aggression was higher than female-initiated aggression (P3a), but that there was no effect of habitat type on the frequency of female-initiated aggression (P3b, Figure 4.4; Table 4.3). Finally, as I predicted, female-initiated aggressive interactions tended to be non-contact, whereas male-initiated aggressive interactions tended to be contact interactions with other males (P3c, Figure 4.1; Table 4.3). Model fit was relatively low ($R2_m = 0.17$; $R2_c = 0.18$), indicating limited explanatory power of the models used to test the interference competition hypothesis (Table 4.3).

4.4.2 Male harassment hypothesis

In support of the male harassment hypothesis, I found the frequency of male harassment increased as a function of group size (P4a; Figure 4.5a), but not sex ratio (P4b; Figure 4.5b, Table 4.4). There was no effect of habitat type on the frequency of male harassment (Table 4.4). However, the relationship between frequency of harassment and group size differed based on habitat type, with a more prominent effect in enhanced habitats (Figure 4.5; Table 4.4).

4.5 Discussion

I observed aggressive interactions among caribou and tested the interference competition and male harassment hypotheses in the context of variation in the social and physical environments. The interference competition hypothesis influences a variety of ecological patterns, including density-dependent habitat selection and population dynamics (Bonenfant et al. 2009), and I present a bottom-up examination of how the physical and social environments influence

variation in aggression and competition. Interference competition predicts a reduction in foraging activities and an increase in female-initiated aggression as group size increases. Despite relatively high frequency of aggressive interactions among and between male and female caribou, I found limited evidence for the interference competition hypothesis. The male harassment hypothesis predicts an increase in male harassment of females as group size increases and I found strong support for this prediction, although I found no effect of habitat on male harassment. My examination of behavioural interactions within and between males and females revealed sex-specific differences in the type of aggressive interactions as well as an effect of the social environment on male harassment.

In partial support of the male harassment hypothesis, I found male harassment increased as a function of group size (P4a), but not sex ratio (P4b). Furthermore, the effect of group size was stronger in enhanced habitats compared to natural habitats (P4c). In damsel flies (*Ischnura elegans*), male harassment of females increased as a function of density (Gosden and Svensson 2009). An important consequence for females is lost foraging opportunities. As groups increase in size and male harassment of females increases, the proximate costs for females could be changes in patterns of movement (L'Italien et al. 2012) or reductions in body condition (Holand et al. 2006). Ultimately, male harassment of females can also result in death, as for example has been observed in feral sheep *Ovis aries* (Reale et al. 1996). Following optimal group size theory (Sibly 1983), females may form intermediate sized groups to reduce the potential for male harassment, while still gaining benefits from social aggregation (Chapter 5). Further, I was unable to test some additional predictions associated with the male harassment hypothesis including the prediction that, at least in ungulates, younger males are more likely to harass females (Reale et al. 1996; Holand et al. 2006; Uccheddu et al. 2015). However, because my

study was conducted after the rut, dominant, and therefore older males (Barrette and Vandal 1990), are expected to reduce mating-related activities (Body et al. 2014) and it is likely that the majority of male harassment I observed was initiated by younger males. The consequences of male harassment for females range from disruption of foraging to death and my results provide support for an effect of the social and physical environments on male harassment.

Consistent with the expectation that males tend to be more aggressive than females (Clutton-Brock and Huchard 2013a), I found the frequency of male-initiated aggression was higher than female-initiated aggression (P3a). Higher frequency of male-initiated aggression was as a direct result of sparring between males, i.e. male-male aggression, which is likely related to maintenance of dominance among males (Barrette and Vandal 1990) or possibly competition among males for late-rut mating opportunities (Airst and Lingle 2019). For female ungulates, competition tends to result in threats rather than physical attacks (Thouless and Guinness 1986), and as I predicted (P3c), I found that females were more likely to engage in non-contact interactions.

Although female-initiated aggression was less common, I found no effect of habitat type on female-initiated aggression (P3b), although I found that the proportion of foraging animals is higher in enhanced compared to natural habitats (P1a – see next paragraph). Based on the assumption that food quality is higher in enhanced habitats, I predicted that female-initiated aggression, and therefore competition, would be higher in enhanced habitats. One possible explanation is that caribou foraging in enhanced habitats prioritize foraging and avoid competition. Although the total area of enhanced habitat in my study area is small, once caribou occupy the enhanced habitat, it is homogeneous and high quality, suggesting that individuals could space out and effectively forage, while also avoiding competition with conspecifics. In

addition, heightened foraging rate in enhanced habitats could be explained by fine-scale density dependence. Foraging in enhanced habitat was restricted due to the size of the area. Local density (animals per unit area) was therefore higher in enhanced compared to natural habitats, even if group size was the same. For red deer, competition for resources in higher and lower quality foraging areas was density-dependent such that competition was predicted to increase as a function of forage quality and density (McLoughlin et al. 2006; Stopher et al. 2012).

Our natural experimental comparison does not support the interference competition hypothesis (P2a and P2b). Given the foraging benefits associated with selecting enhanced habitat, my findings support the idea of a risk-reward trade-off. Risks include harassment from males, but not interference competition, as well as the possibility of human encounters. While human encounters have potential to result in direct mortality (e.g., as a result of vehicle collisions), caribou likely face greater threat from coyote (i.e. the only natural predator on Fogo Island). Although coyotes tend to be acclimated to anthropogenic disturbance (Ellington and Gehrt 2019), coyotes on Fogo Island tend to avoid anthropogenic areas (Huang 2019) where enhanced foraging opportunities for caribou exist. The relationship between caribou and their use of anthropogenic areas has several non-mutually exclusive explanations. First, Fogo Island caribou may take advantage of a 'human shield' and therefore, foraging in artificially enhanced areas does not have the same risk as predicted based on optimal foraging theory. Similarly, predator responses of white-tailed deer (*Odocoileus virginianus*) living in densely populated urban areas was limited, presumably due to lack of predation risk in the urban environment (Richardson and Weckerly 2007). Second, while humans pose some direct risk to Fogo Island caribou, the risk is largely non-consumptive (although the exception is death as a result of vehicle collisions), suggesting the possibility that caribou on Fogo Island have become

habituated to human interactions. Similarly, in Gaspésie National Park, caribou show some familiarity and habituation to humans (Lesmerises et al. 2017). Taken together, these findings highlight the possibility that the physical environment (i.e. enhanced compared to natural habitats) may have a stronger effect on the vigilance-foraging trade-off than the social environment as measured by group size.

Our results provide some insight into caribou mating systems. Unlike during the rut when solitary females are more prone to male harassment (Clutton-Brock et al. 1992), I found an increase in harassment as a function of group size after the rut. One explanation is that as the rut ends, sub-groups merge and form larger mixed-sex groups, resulting in the first exposure of females to younger or lower ranking males. Another possibility is that because younger males are excluded from harems during the rut and have less well developed social rutting behaviour (Clutton-Brock et al. 1992), there may be a second, smaller rut where mating tactics change independent of group size (Bowyer et al. 2020). Although I did not observe copulation, I have observed relatively late births in spring in my system (Bonar et al. 2017), providing some evidence for a second rut. For reindeer, male mating behaviour changed from mate guarding in a harem system (single male, multiple females) to a tending mating tactic (single male, single female) in a smaller second rut (Weladji et al. 2017). Future studies should leverage my examination of male harassment by examining the temporal dynamics of rutting behaviour and quantifying the likelihood of paternity of males that vary in age, size, and dominance.

While I found mixed support for my hypotheses, I wish to acknowledge some logistical and biological caveats that could explain some of my findings. I identified an effect of video length on the frequency of aggressive interactions, where longer videos tended to yield more aggressive interactions. Intuitively, this result makes sense and I account for potential bias by

including duration of videos as a fixed effect and video identity as a random effect in my models. An important caveat is that my comparison of caribou behaviour in natural and enhanced habitats relies on the assumption that forage quality is higher in enhanced habitats due to regular fertilization by humans. I note this was an imperfect test with only a single replicate of enhanced habitat area which is also restricted to only my study system. Despite these restrictions, my study contributes to the body of literature assessing intra-specific variation in caribou aggression and competition. Future studies should aim to quantify natural variation in forage quality and quantity, for example using ecological stoichiometry, and assess the effect of these parameters on behaviour (Leroux et al. 2017). Finally, my inability to identify individuals prevented us from further testing the potential for dominance hierarchies within my system. Previous work on caribou suggests the existence of linear hierarchies (Barrette and Vandal 1986, 1990; Hirotani 1990), and this could explain additional variation in the frequency of aggression, and therefore competition, in caribou.

Our study examined the effects of the social and physical environments on competition and male harassment in caribou. I found support for the male harassment hypothesis and limited support for the interference competition hypothesis. Despite limited support for interference competition, high levels of male harassment, suggests potential for somatic costs to females. Female caribou are prone to incurring the costs of competition in the form of aggression from other females as well as harassment from males. The tension between the effects of the social and physical environment could moderate these costs if female caribou select habitats and social groups that minimize competition with other females and harassment from males.

4.6 Acknowledgements

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Table 4.1: Ethogram of six aggression-related behaviours quantified in video recordings of caribou (*Rangifer tarandus*) on Fogo Island in the autumns of 2017–2019.

Behaviour	**Description**
Displacement	One caribou moves towards another and displaces it from foraging. Displacement is separated into sub-categories that include displacement with physical contact and displacement without physical contact.
Sparring	From standing positions, two caribou make contact with antlers. Sparring is separated into three sub-categories where: 1) sparring is brief (<3 seconds); 2) sparring occurs for a moderate period of time (3–10 seconds) and it is clear both animals are exerting effort; 3) sparring occurs for an extended period of time (>10 seconds), both animals are lunging towards each other, and it is clear both animals are exerting considerable effort. In cases, where sparring lasted >10 seconds, I considered new sparring events to occur when both individuals disengaged for at least 3 seconds and moved away from one another before beginning again.
Head butt	From a standing position, one caribou makes contact, or attempted contact, with another using their head. Head butting is separated into sub-categories that include head butts with physical contact and head butts without physical contact.
Kicking	From a standing position, one caribou approaches another and raises a front leg in a kicking motion. Kicking is separated into sub-categories that include kicking with physical contact and kicking without physical contact.
Rearing	One caribou stands up on hind legs and lunges towards another caribou. Rearing is separated into two sub-categories where only the initiator rears (category 1) or both the initiator and the other caribou rear (category 2). Within each sub-category, rearing is further separated into sub-categories that include rearing with physical contact and rearing without physical contact.
Harassment	Harassment took two different forms. First, in cases where a male caribou attempted, but failed, to mount a female caribou from behind. Second, in cases where a male caribou chased or smelled the vulva of a female caribou. Importantly, mounting and chasing did not include mating and these behaviours represented a non-mating form of harassment.

Table 4.2: Summary of beta regression models testing the effects of habitat type (enhanced or natural) and group size on the proportion of time groups of caribou (*Rangifer tarandus*) spent on vigilant and foraging, group identity and year as random effects. I included data from 691 scan observations over 41 video observation periods in these models. Reference category for habitat is enhanced habitat.

	Vigilance			**Foraging**		
Fixed effect	**Coefficient ± se**	**t-value**	**p-value**	**Coefficient ± se**	**t-value**	**p-value**
Intercept	–1.97 ± 0.36	–5.69	**<0.001**	1.64 ± 0.31	5.34	**<0.001**
Habitat	–0.008 ± 0.31	0.37	0.97	–0.70 ± 0.26	–2.72	**0.007**
Group size	0.02 ± 0.009	1.56	0.06	–0.008 ± 0.008	–0.97	0.33
Random effect	**Variance (± SD)**			**Variance (± SD)**		
Group identity	0.40 ± 0.63			0.19 ± 0.41		
Year	$0.23 \times 10^{-10} \pm 0.15 \times 10^{-5}$			$0.43 \times 10^{-11} \pm 0.21 \times 10^{-6}$		

Table 4.3: Summary of a general linear mixed model testing the effect of habitat type (enhanced or natural), sex of the caribou initiating the interaction (male or female), and behavioural type (contact or non-contact) on the log-transformed rate of aggression towards other caribou (*Rangifer tarandus*). I included 481 aggressive interactions over 36 video observation periods that were pooled for analysis with the number of interactions in each video as the response variable in the model. The model was fit with a Poisson distribution and I included video identity as a random effect. The marginal R2 value is the variance explained by fixed effects ($R2_m$ = 0.17) and conditional R2 is the variance explained by random effects ($R2_c$ = 0.18). Reference category for habitat is enhanced habitat; for sex is female; and for behaviour is contact behaviours; and for year is 2017.

Fixed Effects	**Coefficient ± se**	**z-value**	**p-value**
Intercept	–0.22 ± 0.67	–0.33	0.74
Habitat	–0.58 ± 0.54	–1.07	0.28
Sex	–2.27 ± 0.53	–4.30	**<0.001**
Behaviour	0.49 ± 0.25	1.93	**0.05**
Group size	0.009 ± 0.01	0.86	0.39
Duration of Video	0.05 ± 0.025	2.10	**0.03**
Year			
-2018	–0.12 ± 0.36	–0.32	0.75
-2019	–0.18 ± 0.35	–0.52	0.60
Habitat * Sex	–0.34 ± 0.52	–0.66	0.51
Behaviour * Sex	1.63 ± 0.57	2.85	**0.004**
Habitat * Group size	0.01 ± 0.02	0.55	0.57
Random Effects	Variance ± SD		
Video Identity	0.052 ± 0.23		
Group Identity	$0.63 \times 10^{-8} \pm 0.0002$		

Table 4.4: Summary of generalized linear mixed effect model testing the effect of habitat, group size, and sex ratio on the rate of male harassment towards female caribou (*Rangifer tarandus*). I included 166 male harassment interactions over 36 video observation periods that were pooled for analysis with the number of interactions in each video as the response variable in the model. The model was fit with a negative binomial distribution. The reference category is enhanced habitat.

Fixed effects	**Coefficient ± se**	**z-value**	**p-value**
Intercept	–2.29 ± 1.28	–1.78	0.07
Habitat	–0.37 ± 1.12	–0.33	0.74
Group size	0.05 ± 0.02	3.32	**0.0008**
Sex ratio	0.54 ± 1.98	0.27	0.78
Duration	0.09 ± 0.04	2.14	**0.03**
Year			
-2018	0.47 ± 0.64	0.73	0.47
-2019	0.96 ± 0.62	1.56	0.12
Habitat*Group size	–0.025 ± 0.02	–1.13	0.26
Habitat*Sex ratio	2.94 ± 4.11	0.72	0.47
Random effects	**Variance (± SD)**		
Video identity	0.25 ± 0.50		

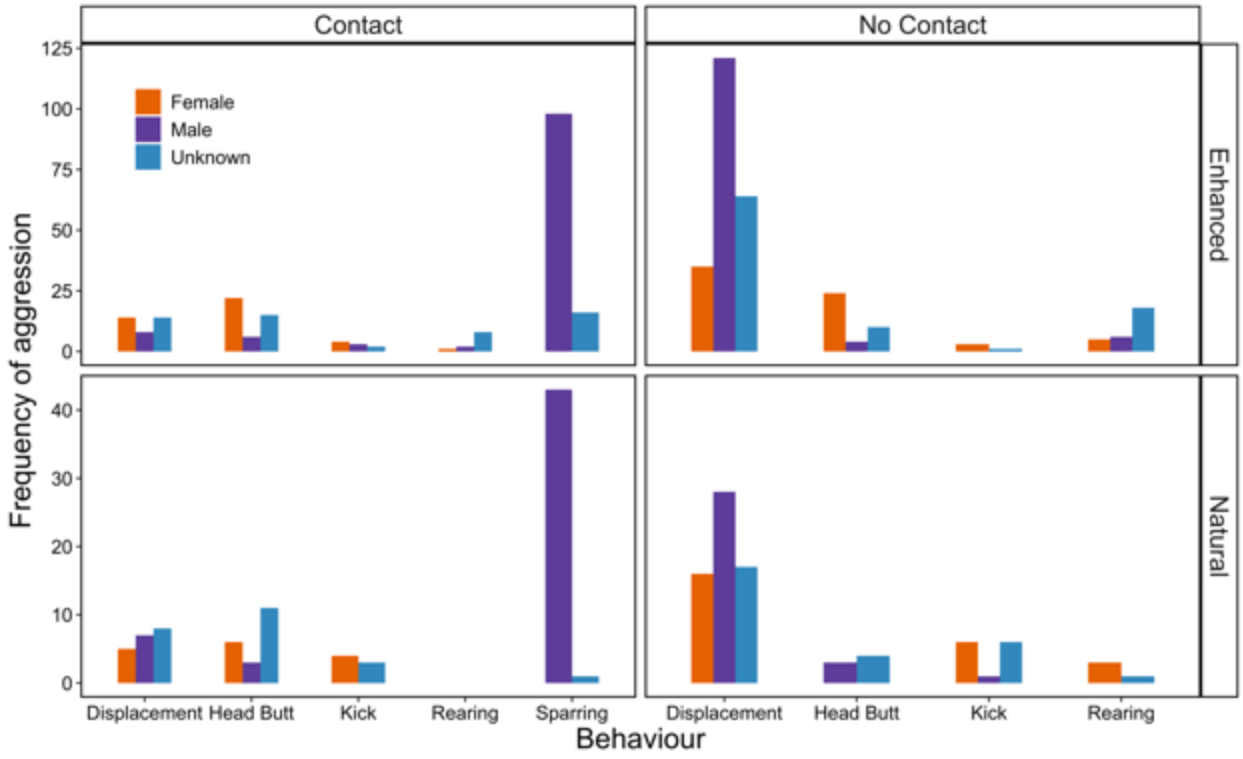

Figure 4.1: Summary of the total number of different types aggressive behaviours (n = 848 total observations) for female (orange bars) and male (purple bars) caribou (*Rangifer tarandus*) directed towards males and females. Blue bars denote cases where the sex of the initiating caribou was unknown. Contact and non-contact aggressive interactions (see Table 4.1 for definitions) were separated between enhanced and natural habitat types observed for caribou. Note the difference in the y-axis extent for enhanced and natural habitats and that sparring interactions were only deemed to be contact interactions.

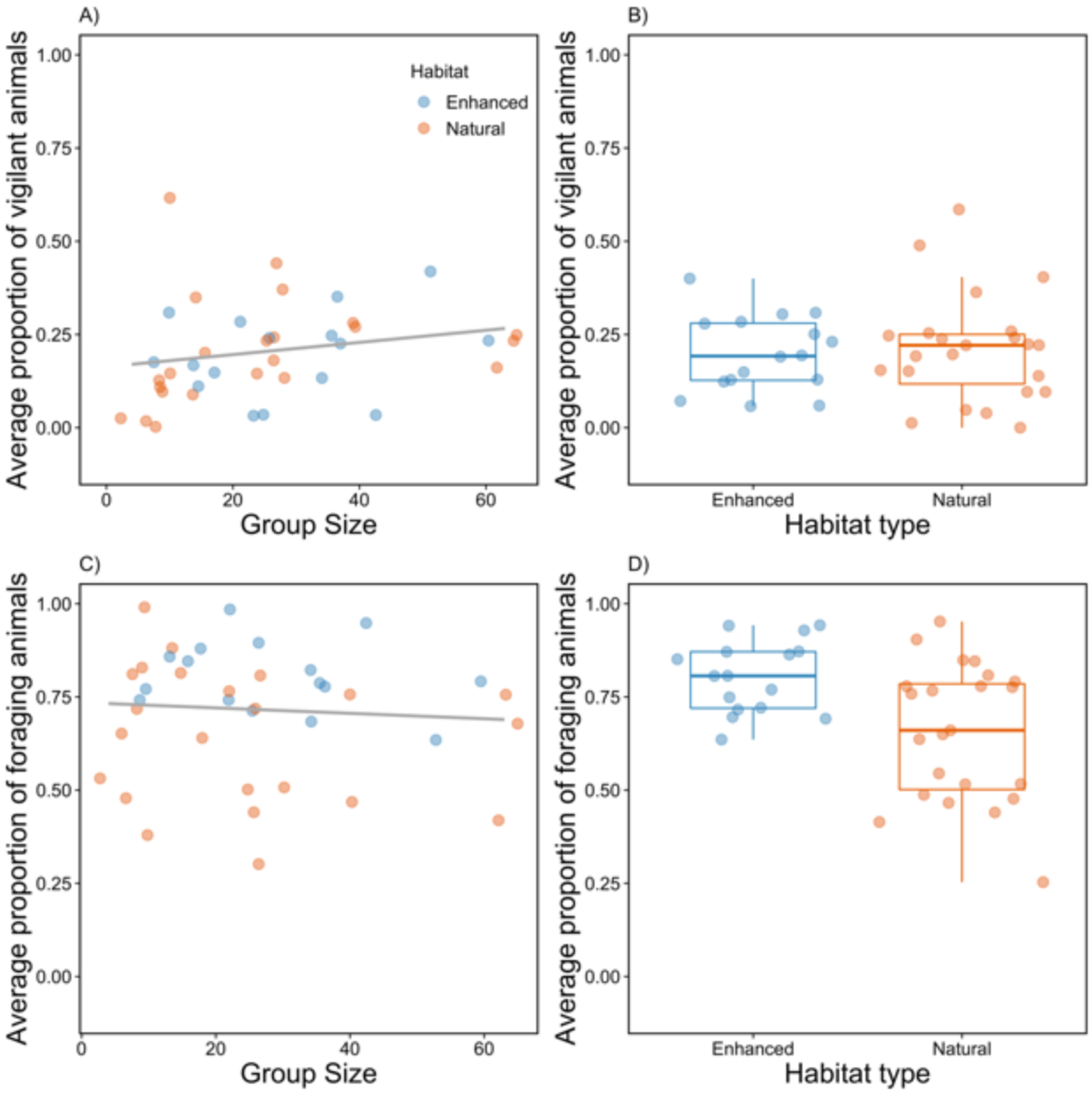

Figure 4.2: Relationship between average proportion of vigilant (Panels A and B) and foraging (Panels C and D) animals and group size in enhanced (blue points) and natural (orange points) habitat types for caribou (*Rangifer tarandus*). Averages were calculated for 41 video recorded focal observations.

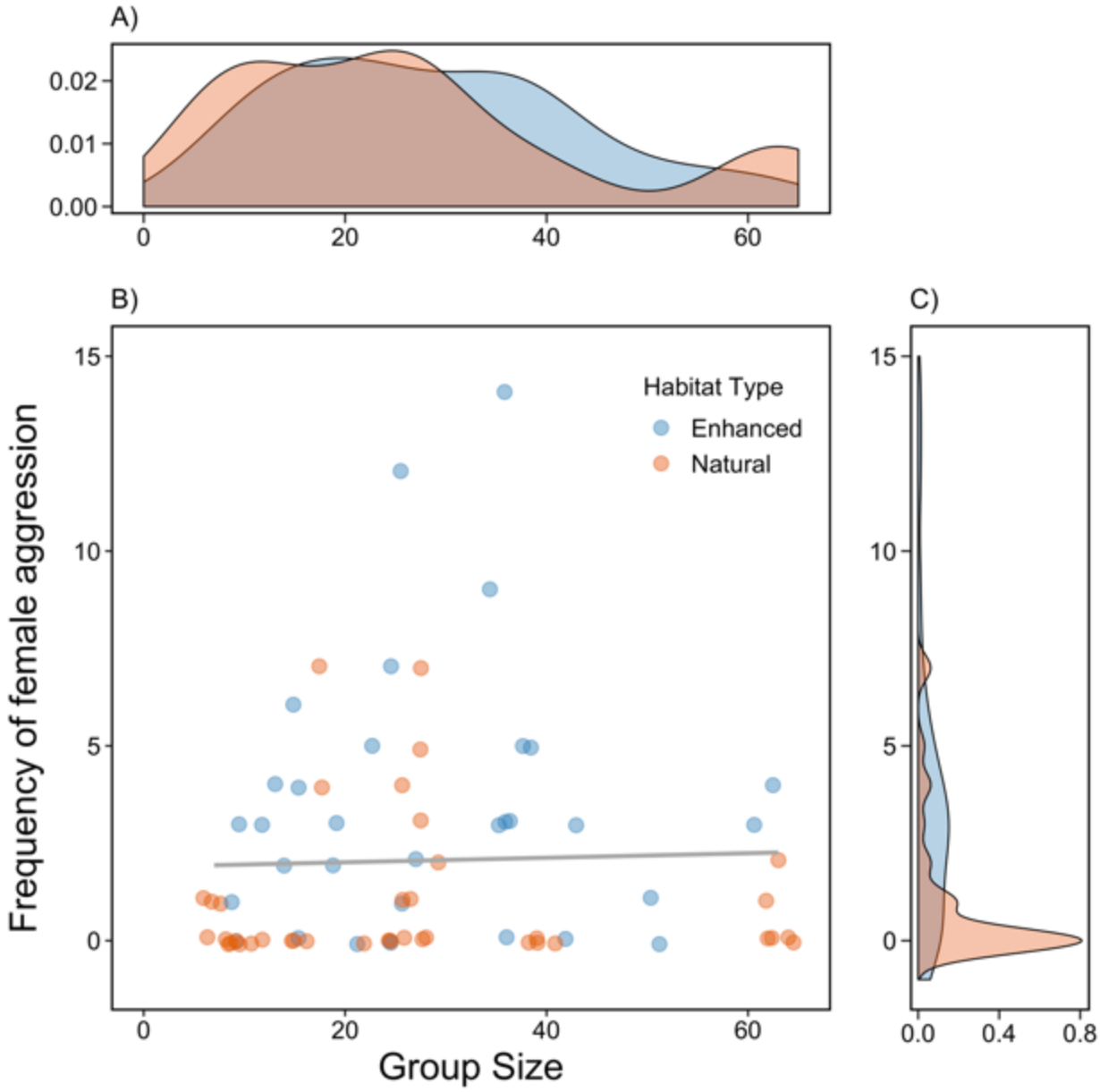

Figure 4.3: Relationship between group size and total frequency of female-female aggression per video for caribou (*Rangifer tarandus*) in natural (blue dots) and enhanced (orange dots) habitats (Panel B). Panel A displays the frequency distribution for group size observations in each habitat type, while Panel C displays the frequency distribution for female aggression in each habitat type.

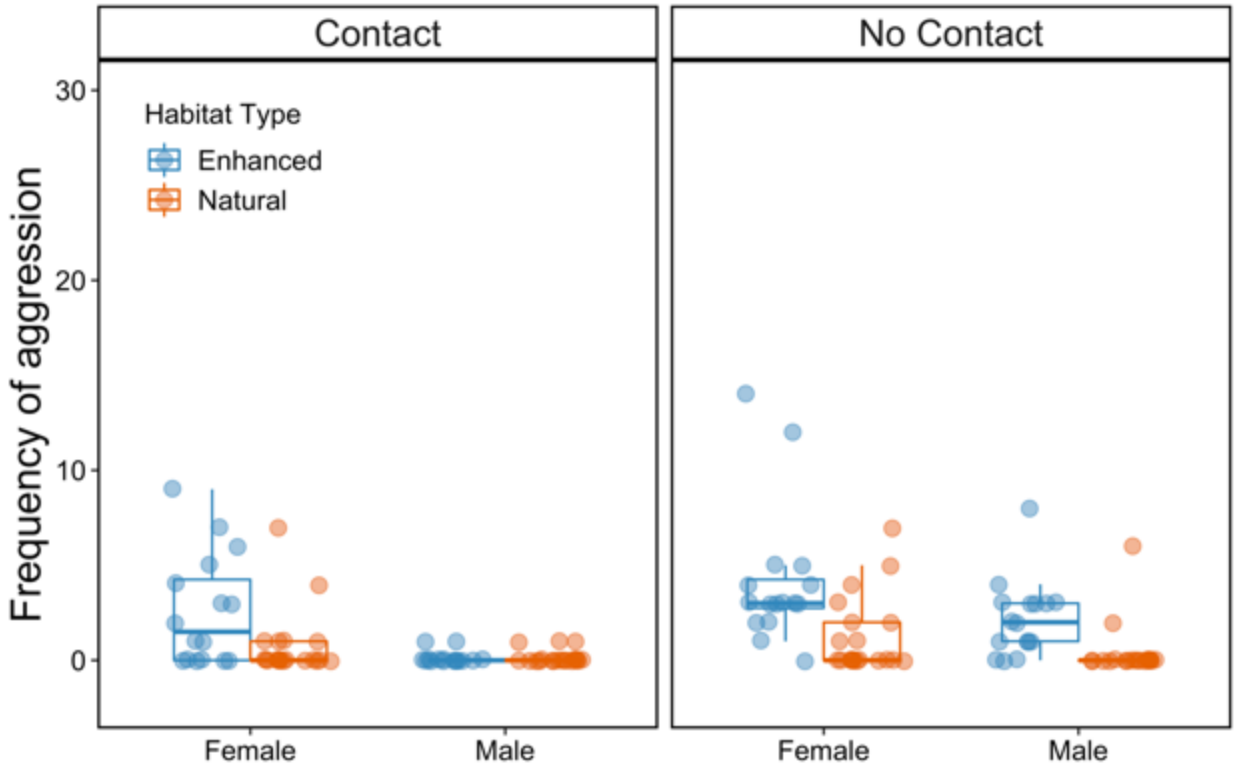

Figure 4.4: Relationship between total frequency of aggression per video separated into contact (orange boxes and points) and non-contact (purple boxes and points) interactions among caribou (*Rangifer tarandus*). Contact interactions are those in which two caribou physically contacted one another and non-contact interactions are those in which two caribou interacted but did not come in physical contact with one another (see Table 4.1 for detailed definitions). Total number of interactions per video were calculated for instances when male (n = 163 total non-contact interactions; n = 170 total contact interactions) and female (n = 92 total non-contact interactions; n = 56 contact interactions) caribou initiated interactions in enhanced (n = 390 male-initiated interactions; n = 108 female-initiated interactions) and natural habitats (n = 109 male-initiated interactions; 40 female-initiated interactions).

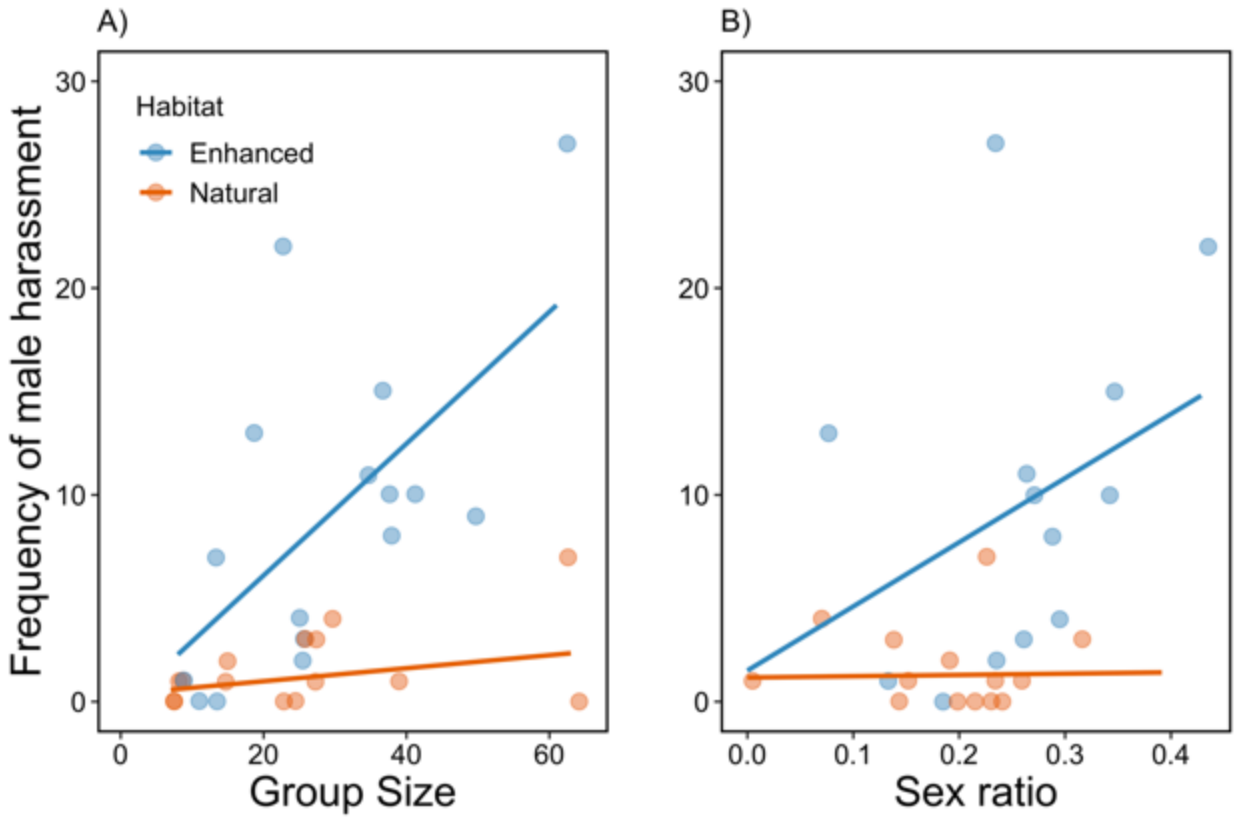

Figure 4.5: Relationship between A) group size and total frequency of male harassment of female caribou (*Rangifer tarandus*) per video in natural (orange) and enhanced (blue) habitats (n = 175 harassment events); and B) sex ratio, defined as the ratio of adult males to females, and total frequency of male harassment per video.

4.7 References

Airst J, Lingle S (2019) Courtship strategies of white-tailed deer and mule deer males when living in sympatry. Behaviour 156:307–330. doi: 10.1163/1568539X-00003543

Barrette C, Vandal D (1986) Social rank, dominance, antler size, and access to food in snow-bound wild woodland caribou. Behaviour 97:118–145

Barrette C, Vandal D (1990) Sparring, relative antler size, and assessment in male caribou. Behav Ecol Sociobiol 26:383–387

Bergerud AT (1974a) Relative abundance of food in winter for Newfoundland caribou. Oikos 25:379–387

Bergerud AT (1974b) Rutting behaviour of Newfoundland caribou. Behav ungulates its Relat to Manag 1:395–435

Bergerud AT, Mercer WE (1989) Caribou introductions in eastern North America. Wildl Soc Bull 17:111–120

Body G, Weladji RB, Holand Ø, Nieminen M (2014) Highly competitive reindeer males control female behavior during the rut. PLoS One 9:e95618. doi: 10.1371/journal.pone.0095618

Bonar M, Laforge MP, Wal E Vander (2017) Observation of a $p < 10 - 9$ life-history event : implications of record-late caribou birth on ungulate reproductive ecology and field studies. Can Jounal Zool 137:133–137

Bonenfant C, Gaillard JM, Coulson T, et al (2009) Empirical evidence of density-dependence in populations of large herbivores. Adv Ecol Res 41:313–357. doi: 10.1016/S0065-2504(09)00405-X

Bowyer RT, Mccullough DR, Rachlow JL, et al (2020) Evolution of ungulate mating systems: Integrating social and environmental factors. Ecol Evol 1–19. doi: 10.1002/ece3.6246

Brooks ME, Kristensen K, van Benthem KJ, et al (2017) glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. R J 9:378–400. doi: 10.32614/rj-2017-066

Cassidy KA, Macnulty DR, Stahler DR, et al (2015) Group composition effects on aggressive interpack interactions of gray wolves in Yellowstone National Park. Behav Ecol 26:1352–1360. doi: 10.1093/beheco/arv081

Chamaillé-Jammes S, Fritz H, Valeix M, et al (2008) Resource variability, aggregation and direct density dependence in an open context: The local regulation of an African elephant population. J Anim Ecol 77:135–144. doi: 10.1111/j.1365-2656.2007.01307.x

Clutton-Brock T, Huchard E (2013a) Social competition and its consequences in female mammals. J Zool 289:151–171. doi: 10.1111/jzo.12023

Clutton-Brock TH, Albon SD, Gibson RM, Guinness FE (1979) The Logical Stag: adaptive aspects of fighting in red deer (*Cervus elaphus L.*). Anim Behav 27:211–225. doi: 10.2307/3492065

Clutton-Brock TH, Huchard E (2013b) Social competition and selection in males and females. Philos Trans R Soc B Biol Sci 368:. doi: 10.1098/rstb.2013.0074

Clutton-Brock TH, Price OF, Maccoll ADC (1992) Mate retention, harassment, and the evolution of ungulate leks. Behav Ecol 3:234–242. doi: 10.1093/beheco/3.3.234

Cresswell W (1998) Variation in the strength of interference competition with resource density in blackbirds, *Turdus merula*. Oikos 81:152–160. doi: 10.2307/3546477

Douma JC, Weedon JT (2019) Analysing continuous proportions in ecology and evolution: A practical introduction to beta and Dirichlet regression. Methods Ecol Evol 10:1412–1430. doi: 10.1111/2041-210X.13234

Ellington EH, Gehrt SD (2019) Behavioral responses by an apex predator to urbanization. Behav Ecol 30:821–829. doi: 10.1093/beheco/arz019

Folmer EO, Olff H, Piersma T (2012) The spatial distribution of flocking foragers: Disentangling the effects of food availability, interference and conspecific attraction by means of spatial autoregressive modeling. Oikos 121:551–561. doi: 10.1111/j.1600-0706.2011.19739.x

Fournier F, Festa-Bianchet M (1995) Social dominance in adult female mountain goats. Anim Behav 49:1449–1459. doi: 10.1016/0003-3472(95)90066-7

Gosden TP, Svensson EI (2009) Density-dependent male mating harassment, female resistance, and male mimicry. Am Nat 173:709–721. doi: 10.1086/598491

Goss-Custard JD (1980) Competition for food and interference among waders. Ardea 68:31–52

Hall MJ (1983) Social organization in an enclosed group of red deer (Cervus elaphus L.) on Rhum. Z Tierpsychol 61:250–262. doi: 10.1111/j.1439-0310.1983.tb01341.x

Hirotani A (1990) Social organization of reindeer (*Rangifer tarandus*), with a special reference to relationships among females. Can J Zool 68:743–749

Hirsch BT (2007) Costs and benefits of within-group spatial position: a feeding competition model. Q Rev Biol 82:9–27

Holand, Weladji RB, Røed KH, et al (2006) Male age structure influences females' mass change during rut in a polygynous ungulate: The reindeer (*Rangifer tarandus*). Behav Ecol

Sociobiol 59:682–688. doi: 10.1007/s00265-005-0097-5

Huang RKK (2019) Strategies for sharing space in a predator-prey relationship: drivers for local coyote (*Canis latrans*) and caribou (*Rangifer tarandus*). Memorial University of Newfoundland

Isvaran K (2005) Variation in male mating behaviour within ungulate populations: Patterns and processes. Curr Sci 89:1192–1199

Kasozi H, Montgomery RA (2020) Variability in the estimation of ungulate group sizes complicates ecological inference. Ecol Evol 1–9. doi: 10.1002/ece3.6463

L'Italien L, Weladji RB, Holand Ø, et al (2012) Mating group size and stability in reindeer *Rangifer tarandus*: The effects of male characteristics, sex ratio and male age structure. Ethology 118:783–792. doi: 10.1111/j.1439-0310.2012.02073.x

Leroux SJ, Vander Wal E, Wiersma YF, Hermanutz L (2017) Stoichiometric distribution models: Ecological stoichiometry at the landscape scale. Ecol Lett 20:1495–1506. doi: 10.1111/ele.12859

Lesmerises F, Déry F, Johnson CJ, St-Laurent MH (2018a) Spatiotemporal response of mountain caribou to the intensity of backcountry skiing. Biol Conserv 217:149–156. doi: 10.1016/j.biocon.2017.10.030

Lesmerises F, Johnson CJ, St-Laurent M-H (2018b) Landscape knowledge is an important driver of the fission dynamics of an alpine ungulate. Anim Behav 140:39–47. doi: 10.1016/j.anbehav.2018.03.014

Lesmerises F, Johnson CJ, St-Laurent MH (2017) Refuge or predation risk? Alternate ways to perceive hiker disturbance based on maternal state of female caribou. Ecol Evol 7:845–854. doi: 10.1002/ece3.2672

Lewis KP, Mahoney SP (2014) Caribou survival, fate, and cause of mortality in Newfoundland: a summary and analysis of the patterns and causes of caribou survival and mortality in Newfoundland during a period of rapid population decline (2003-2012). Tech Bull No 009, Sustain Dev Strateg Sci Gov Newfoundl Labrador, St John's, NL

Lima SL (1995) Back to the basics of anti-predatory vigilance: the group-size effect. Anim Behav 49:11–20

Mahoney SP, Virgl JA (2003) Habitat selection and demography of a nonmigratory woodland caribou population in Newfoundland. Can J Zool 81:321–334. doi: 10.1139/z02-239

McLoughlin PD, Boyce MS, Coulson T, Clutton-Brock T (2006) Lifetime reproductive success and density-dependent, multi-variable resource selection. Proc R Soc B 273:1449–1454. doi: 10.1098/rspb.2006.3486

Peignier M, Webber QMR, Koen EL, et al (2019) Space use and social association in a gregarious ungulate: Testing the conspecific attraction and resource dispersion hypotheses. Ecol Evol 9:5133–5145. doi: 10.1002/ece3.5071

Peterson LM, Weckerly FW (2018) Social behavior and changes in foraging behavior in a gregarious ungulate. J Mammal 99:1422–1429. doi: 10.1093/jmammal/gyy129

R Core Team (2019) R: A language and environment for statistical computing

Rayl ND, Fuller TK, Organ JF, et al (2014) Mapping the distribution of a prey resource: neonate caribou in Newfoundland. J Mammal 95:328–339. doi: 10.1644/13-MAMM-A-133.1

Reale D, Bousses P, Chapuis JL (1996) Female-biased mortality induced by male sexual harassment in a feral sheep population. Can J Zool 74:1812–1818. doi: 10.1139/z96-202

Richardson KE, Weckerly FW (2007) Intersexual social behavior of urban white-tailed deer and its evolutionary implications. Can J Zool 85:759–766. doi: 10.1139/Z07-057

Sansom A, Cresswell W, Minderman J, Lind J (2008) Vigilance benefits and competition costs in groups: do individual redshanks gain an overall foraging benefit? Anim Behav 75:1869–1875. doi: 10.1016/j.anbehav.2007.11.005

Schaefer JA, Mahoney SP, Weir JN, et al (2016) Decades of habitat use reveal food limitation of Newfoundland caribou. J Mammal 97:386–393. doi: 10.1093/jmammal/gyv184

Sibly RM (1983) Optimal group size is unstable. Anim Behav 31:947–948

Siracusa E, Morandini M, Boutin S, et al (2017) Red squirrel territorial vocalizations deter intrusions by conspecific rivals. Behaviour 154:1259–1273. doi: 10.1163/1568539X-00003467

Stopher K V, Walling CA, Morris A, et al (2012) Shared spatial effects on quantitative genetic parameters: accounting for spatial autocorrelation and home range overlap reduces estimates of heritability in wild red deer. Evolution (N Y) 66:2411–2426. doi: 10.1111/j.1558-5646.2012.01620.x

Stutz RS, Bergvall UA, Leimar O, et al (2018) Cohesiveness reduces foraging efficiency in a social herbivore. Anim Behav 135:57–68. doi: 10.1016/j.anbehav.2017.11.004

Tennenhouse EM, Weladji RB, Holand O, et al (2011) Mating group composition influences somatic costs and activity in rutting dominant male reindeer (*Rangifer tarandus*). Behav Ecol Sociobiol 65:287–295. doi: 10.1007/s00265-01

Thouless CR, Guinness FE (1986) Conflict between red deer hinds: the winner always wins. Anim Behav 34:1166–1171

Tobler M, Schlupp I, Plath M (2011) Costly interactions between the sexes: Combined effects of male sexual harassment and female choice? Behav Ecol 22:723–729. doi: 10.1093/beheco/arr044

Uccheddu S, Body G, Weladji RB, et al (2015) Foraging competition in larger groups overrides harassment avoidance benefits in female reindeer (*Rangifer tarandus*). Oecologia 179:711–718

Veiberg V, Loe LE, Mysterud A, et al (2004) Social rank, feeding and winter weight loss in red deer: Any evidence of interference competition? Oecologia 138:135–142. doi: 10.1007/s00442-003-1399-9

Webber QMR, Vander Wal E (2018) An evolutionary framework outlining the integration of individual social and spatial ecology. J Anim Ecol 87:113–127. doi: 10.1111/1365-2656.12773

Weckerly FW, Ricca MA, Giguere N (2014) Aggression and Coexistence in Female Caribou. Arctic 67:189–195

Weladji RB, Body G, Holand Ø, et al (2017) Temporal variation in the operational sex ratio and male mating behaviours in reindeer (*Rangifer tarandus*). Behav Processes 140:96–103. doi: 10.1016/j.beproc.2017.04.011

West-Eberhard MJ (1979) Sexual Selection, Social Competition, and Evolution. Proc Am Philos Soc 123:222–234

Witter LA, Johnson CJ, Croft B, et al (2012) Behavioural trade-offs in response to external stimuli: Time allocation of an Arctic ungulate during varying intensities of harassment by parasitic flies. J Anim Ecol 81:284–295. doi: 10.1111/j.1365-2656.2011.01905.x

CHAPTER 5:CONTEXT-DEPENDENT GROUP SIZE: EFFECTS OF POPULATION DENSITY, HABITAT, AND SEASON

Submitted as: Webber QMR, Vander Wal E. Context-dependent group size: effects of population density, habitat, and season. *Behavioral Ecology.*

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5.1 Abstract

Group size can vary in relation to population density as well as habitat and season; the latter two factors may interact with population density to affect group size due to variation in the foraging-related benefits of social aggregation in different habitats and seasons. I tested the hypothesis that group size varies across ecological contexts, including population density, habitat type, and season, for woodland caribou (*Rangifer tarandus*) in ten herds over 25 years in Newfoundland, Canada. I predicted that group size would increase as a function of population density. Based on the foraging-related benefits of social aggregation, I predicted larger groups in open habitats because these areas tend to have higher quality foraging resources. I also predicted larger groups during winter because resources are more patchily distributed in winter compared to the rest of the year and animals in groups are expected to exploit social information about the location of foraging resources. In contrast to my prediction, group size decreased as a function of population density. In support of my prediction, group size was larger in winter than calving and summer, but, in contrast to my prediction, it did not vary significantly between open and closed habitats. Patterns of animal grouping are context-dependent and, at least for fission-fusion species, animal groups vary in their size based on the implicit trade-offs between competition, predation risk, and profitability.

Key words: Group size, population density, demography, social information, woodland caribou, *Rangifer tarandus*

5.2 Introduction

Variation in an animal's social environment, i.e. the size and composition of social groups, occurs as individuals balance the costs and benefits of group living to maximize fitness (Silk 2007). Benefits associated with group-living include diluted predation risk, information transfer about resources, and access to mating opportunities, while potential costs include competition for resources and risk of pathogen transmission (Hamilton 1964; Alexander 1974; Lima and Dill 1990; Krause and Ruxton 2002). Balancing the costs and benefits of group-living can result in an evolutionarily stable strategy that promotes group sizes to stabilize at an intermediate level (McNamara and Houston 1992). In theory, groups range from two individuals to some maximum size, where fitness of individuals is maximized at an intermediate group size, but fitness of solitary individuals is equal to that of individuals in groups of maximum size (Higashi and Yamamura 1993; Williams et al. 2003). In the context of the costs and benefits of sociality, animals should form groups of optimal size that are large enough to maximize vigilance, but small enough to minimize competition for foraging resources. In theory, groups that meet this balance should have highest fitness. However, criticisms of the optimal group size hypothesis are that groups increase in size beyond the optimal (Williams et al. 2003), for species with fission-fusion dynamics, i.e., merging and splitting of groups through space and time, there is likely no single optimal group size and optima should be context dependent (Sibly 1983; Gerard et al. 2002). Group size could therefore depend on context, and will vary in size based on a species behaviour, ecology, and life-history (Webber and Vander Wal 2018).

In populations with limited immigration and emigration, the number and size of animal groupings is a zero-sum game. Groups can only be as numerous as the total number of animals in the population (Gerard et al. 2002). Population density can therefore influence the size and

number of possible group members in a given area and the emergent result is a dynamic fission-fusion social system where groups merge and split through space and time. Importantly in the context of population density, in fission-fusion societies, group size typically increases with population density. Caughley (1964) posited that populations of large herbivores typically display fission-fusion dynamics and based on the ideal gas law (Higashi and Yamamura 1993), increases in population density should increase the probability of group fusion and therefore average, and potentially optimal, group size. In fission-fusion societies of both Pyrenean chamois (*Rupicarpa pyrenaica*) and elk (*Cervus elaphus*), average group size was positively correlated with population density (Pépin and Gerard 2008; Vander Wal, van Beest, et al. 2013). Despite empirical evidence for a relationship between population density and average group size, Krause and Ruxton (2002) highlighted that average group size should only increase with population density to optimal group size. Beyond the point of optimal group size, they inferred a further increase in population density would result in an increase in the number of groups (Krause and Ruxton 2002).

While group size varies with population density, it is also expected to vary spatially as a function of habitat type and temporally as a function of seasonal variation in forage availability (Fryxell 1991; Barja and Rosellini 2008). The ‘many eyes hypothesis’ suggests that group size increases vigilance and dilutes the per capita risk of being predated compared to closed or forested habitats (McNamara and Houston 1992; Lima 1995). By contrast, in habitats with less profitable resources and where there is greater cover to hide from predators, such as forests or shrublands, observed group size should be relatively small (Creel et al. 2014). In open habitats, the many eyes hypothesis implicitly assumes that group members are able to maintain visual and auditory contact with one another to provide a warning signal should a predator be detected.

Empirical support for the many eyes hypothesis exists in a variety of taxa, for example, in redshanks (*Tringa totanus*), vigilance decreased with group size (Sansom et al. 2008), while in giraffes (*Giraffa camelopardalis*) group size was larger in open habitats compared to mixed woods or closed canopy forests (Muller et al. 2018). As individuals filter (i.e. fission) into habitats of different profitability, density-dependent habitat selection dictates that animals will select habitat such that average fitness is equal across habitats (Webber and Vander Wal 2018). Habitats should therefore have a group size where mean fitness is maximized. For example, in open habitats with profitable resources, individuals face a trade-off between higher quality foraging resources and risk of predation (Sih 1980; Lima and Dill 1990; Brown et al. 1999). Habitat openness is among the most important predictors of group size and the risk-resource trade-off associated with grouping in closed or open habitats is predicted to promote correlated evolutionary trajectory of group size and habitat openness (Jarman 1974; Gerard et al. 2002).

In seasonal environments, access to ephemeral resources should also influence group size. For ungulates, the phenomenon of seasonal variation in social aggregation is widespread (Gerard et al. 2002; Vander Wal, Paquet, et al. 2013). In seasonal environments, conspecific attraction may explain animal grouping patterns because of variation in the availability of foraging resources across seasons. Conspecific attraction is relevant in seasonal (Stamps 1988). For elk, winter group size (Brennan et al. 2015) and inter-individual distances between pairs of individuals (Vander Wal, Paquet, et al. 2013) both increase because individuals aggregate at foraging sites and information about the location and quality of these sites facilitates an increase in group size where resources are concentrated. Meanwhile, when foraging resources are consistently abundant and widespread, group size tends to decrease and individuals often disperse into forested, or closed, habitats to forage (Christianson and Creel 2007). For bison

(*Bison bison*) at sites with higher quality forage, group size increased in winter and decreased in summer due to foraging sites being more difficult to locate under the snow in winter compared to snow-free areas in summer (Fortin and Fortin 2009). Seasonal variation in resource availability should therefore influence aggregation patterns for gregarious animals by influencing movement and habitat selection.

Caribou and reindeer (*Rangifer tarandus*) live in loose fission-fusion societies (Body et al. 2015; Lesmerises et al. 2018) where groups merge and split through space and time. Group sizes for sedentary woodland caribou often do not exceed ten individuals, while group sizes for migratory barren-ground caribou and arctic reindeer can exceed hundreds or even thousands of individuals (Table S5.1). As a species, caribou ecotypes therefore tend to reduce group size as habitats become more closed, i.e., from open tundra to closed boreal forest (Table S5.1; Festa-Bianchet et al. 2011). Despite evidence suggesting that caribou vary in their group sizes both spatially and temporally, the combined effects of population density, habitat type, and season on group size remain under-studied and have potential to influence caribou conservation (Table S5.1). Anthropogenic disturbance affects caribou habitat throughout North America, and environmental change can influence the size and connectivity of groups for caribou (Vistnes and Nellemann 2008) and other gregarious ungulates (Vander Wal et al. 2012; Koen et al. 2017; Sigaud et al. 2017). The social environment is relevant in the context of influence population growth (Snijders et al. 2017; Webber and Vander Wal 2018) and in the case of caribou, the social environment is important because groups benefit from collective vigilance and shared information about access to resources (Peignier et al. 2019). Focused research on grouping patterns in caribou may help attenuate the potential for reduced population growth as a result of disturbance and inform caribou conservation and management.

We studied the combined effects of population density, habitat, and season on group size across nine replicate herds of woodland caribou on the Island of Newfoundland where population density varied over time from 1987 to 2013 (Bastille-Rousseau et al. 2013). I also used one focal herd to study the effects of habitat and season on group size, but where population density was consistent over time. Given that caribou populations are in decline throughout their range, I first tested the hypothesis that group size is density-dependent (Figure 5.1). I predicted that group size will increase as a function of population density for fission-fusion societies because higher density means a greater fusion rate, and therefore larger average group size (Prediction 1a, hereafter P1a). Across a population density gradient, I also predicted the relationship between group size and population density would have a stronger effect size in open habitats (P1b) and in winter (P1c). Second, I tested the hypothesis that, independent of changes in population density, group size is context-dependent. I predicted that, independent of population density, group size would be larger in open compared to closed habitat types (P2a) and group size would be larger in winter and calving compared to summer seasons (P2b). I expected group size would be highest during winter and in open habitats due to limitation of foraging resources and use of social information (Peignier et al. 2019). In addition, I expected group size would be larger in winter when foraging opportunities are relatively scarce, followed by calving when collective vigilance is important to reduce the risk of calf predation, and smallest in summer when foraging opportunities are widespread and calves are mobile enough to out-run predators.

5.3 Methods

5.3.1 Study system and species

Newfoundland is a large island off eastern Canada (47°44’ N, 52°38’ W to 51°44’ N, 59°28’ W) with humid-continental climate and persistent precipitation throughout the year. Natural caribou habitat in Newfoundland consists of black spruce (*Picea mariana*), balsam fir (*Abies balsamea*), and white birch (*Betula papyrifera*) interspersed with bogs, lakes, and barren rock. Within their range in Newfoundland, caribou forage primarily on lichen, grasses, sedges, and other deciduous browse (Bergerud 1974; Mahoney and Virgl 2003; Schaefer et al. 2016). Caribou on Fogo Island, a smaller island off the northeastern coast of the main island, were introduced in the 1960s (Bergerud and Mercer 1989).

In Newfoundland, wolves (*Canis lupus*) were extirpated circa 1920, so invasive coyotes (*Canis latrans*) and native black bears (*Ursus americanus*) are the primary predators of caribou (Bastille-Rousseau, Schaefer, et al. 2016). Coyotes and black bears are responsible for the majority of mortalities for neonate caribou calves (Bastille-Rousseau, Schaefer, et al. 2016), although predation can still occur after the calving period (Lewis and Mahoney 2014). Although predation by coyotes or black bears on adult female caribou is possible, only ca. 6% of adult mortalities were attributed to predation (Lewis and Mahoney 2014).

Similar to elsewhere in their range (Festa-Bianchet et al. 2011; Mallory and Boyce 2017), caribou population sizes on the Island of Newfoundland have declined precipitously since the 1990s (Bastille-Rousseau et al. 2013). Over the last 50 years, caribou herds in Newfoundland have undergone drastic changes in abundance. In the 1960s and 1970s, herds were relatively small, followed by marked increases in the 1980s to mid-1990s, followed by a precipitous decline following the mid-1990s to current lows (Bastille-Rousseau et al. 2013). Population

declines have been attributed to density-dependent nutritional stress on females as well as predation on calves by coyotes and bears (Bastille-Rousseau et al. 2013; Bastille-Rousseau et al. 2016). The Fogo Island herd increased in size from a few dozen individuals in the 1960s to approximately 300 at present but over the last ten years population density has remained stable (Newfoundland and Labrador Wildlife Division unpublished data).

There are approximately 14 large caribou herds in Newfoundland (Morrison et al. 2012) as well as a number of smaller natural and introduced herds (Bergerud and Mercer 1989). Caribou in Newfoundland display relatively high philopatry to their natal herds and calving grounds (Schaefer and Mahoney 2013). Here, I include historic data from nine (see below for data inclusion criteria) large caribou herds in Newfoundland (hereafter, Newfoundland herds: Figure S5.1; Table 5.1) for which population density has changed over the last three decades as well as contemporary data from the Fogo Island herd (hereafter, Fogo herd) for which population density has remained stable.

5.3.2. Group size and population density observations

For the Newfoundland herds, group sizes were recorded during aerial surveys, while for Fogo Island group sizes were recorded during routine fieldwork on foot. The majority of herds in Newfoundland have been monitored and surveyed intermittently since the 1960s. Herds were surveyed in spring or fall using traditional aerial surveys in a systematic strip, random block, stratified-random block or mark-resight design (Mahoney et al. 1998). Specifically, surveys were conducted following a series of line transects over designated herds spaced 1-3 km apart and were flown at an altitude of 150 m above ground level (Mahoney et al. 1998; Fifield et al. 2012). Observation crews typically consisted of at least two observers, but pilots also occasionally acted as secondary observers. Survey data were used to estimate abundance, i.e. population size, which

I use as a proxy for population density (Cattadori et al. 2003; Santini et al. 2018). Abundance is commonly used as a proxy for population density and in the case of caribou in Newfoundland, the possible area available to groups is constant through time. In a given year, it took observers between 1–4 days to survey herds (average = 1.5). Of 189 total surveys that met the criteria for inclusion (see below), 57% (108/189) were conducted in a single day, 30% (57/189) were conducted in two days, 11% (21/189) were conducted in three days, and 1% (3/189) were conducted in four days. Thus, due to the combination of survey design (i.e. stratified-random block) and the period over which surveys were conducted (i.e. ~1-2 days), it is unlikely that individuals or groups were counted twice. I followed Bastille-Rousseau et al. (2016) and delineated survey data into three phases: the increase (1964–1982), the peak (1987–1997), and the decline phases (2001–2013). During aerial surveys, group size, and the demographic composition of caribou were recorded by observers.

Between 2016–2019, group size and composition of caribou groups on Fogo Island were recorded by observers on foot. Groups were determined based on the chain rule, a technique used to assign individuals to groups based on inter-individual distances that 'chain' individuals together based on a threshold distance. In my case, I assumed individuals within 50 m of at least one conspecific were considered in the same group. Thus, if individuals A and B were <50 m apart they would be assigned to the same group. If individual C was <50 m away from B, but >50 m away from A, it would still be assigned to the same group as A and B because C is within 50 m of at least one other group member and the chain rule links all individuals together. The chain rule is widely applied within studies of caribou social and grouping behaviour (Lesmerises et al. 2018; Peignier et al. 2019; Robitaille et al. 2020) and 50 m is a commonly used threshold

for studies of ungulate group size (Kasozi and Montgomery 2020). Groups were categorized based on whether they comprised all females, all males, or a mix of males and females.

Between 1964 and 2013, over 17,000 groups were recorded for 28 caribou herds, including the 14 large herds noted above, on the Island of Newfoundland. Despite the large number of group observations available, I used a series of conservative inclusion criteria to determine which group observations to include. First, although data exist going back to 1964, I only included data from the peak (1987–1997) and decline (2001–2013) phases because data from the first two decades of data collection (i.e. 1964–1986) were sparsely distributed both spatially and temporally. I therefore deemed these data were not comparable to the peak and decline phases where data were more robust. For my comparison of group size across phases, I only included herds that had a minimum of 100 group size observations within each of the peak and decline phases. Second, for my assessment of population density as a predictor of group size (i.e., Prediction 1a) I only included herds that had a minimum of 10 years of survey data. I made one exception to these criteria for the St. Anthony herd, which had only 67 group size observations during the peak phase, but >300 observations during the decline phase (Table 5.1).

In addition to mean group size, I calculated typical group size for each herd-by-year combination. Typical group size is often as either a supplement, or alternative, to mean group size because it characterizes the skewed nature of group size data (Jarman 1974; Reiczigel et al. 2008). Mean group size is the average across groups, whereas typical group size is calculated as the average across individuals. Typical group size is calculated as $\Sigma G_i^2 / \Sigma G_i$ where G is the number of individuals in the ith group. I calculated both mean and typical group size to facilitate comparison to other studies (e.g. Jung et al. 2019) and I assessed the relationship between mean and mean typical group size (Figure S5.2).

5.3.3 Delineating habitat and season

For my assessment of population density and habitat (P1b and P2a) I extracted habitat type from Landsat images with 30x30m pixels based on the location a group was observed. Locations were categorized as one of open (wetland, rocky outcrops, water/ice, and lichen barrens) or closed (conifer scrub, mixed wood, and conifer forest) habitat types for both datasets. During aerial surveys between 2002–2011 for the Newfoundland herds, observers recorded GPS coordinates for a subset of caribou groups observed (P1b). Thus, for subsequent models that include habitat for Newfoundland herds, only data from 2002–2011 were included. During routine fieldwork on Fogo Island, a long-term caribou research program that supports multiple research objectives (Bonar et al. 2018; Peignier et al. 2019), I recorded GPS coordinates for all caribou groups observed.

For my assessment of population density and season (P1c and P2b) as predictors of group size I recorded the date a group was observed. For the Newfoundland herd surveys, I considered data collected between November and March as winter, data collected in May or June as calving, and data collected in September or October as rut. No surveys were conducted in July or August (for details see Mahoney and Weir 2010). For the Fogo Island herd, observations recorded in November and December were considered early winter, observations in May or June were considered calving, and observations in July or August were considered summer. I did not have any observations on Fogo Island in winter (January–March) or the rut (September–October).

5.3.4 Statistical analysis

For all analyses with the Newfoundland caribou herds, I separated herds into relative sizes because herd size varied in size by several orders of magnitude (Table S5.1). To facilitate model convergence, I separated herds into one of three categories: relatively small herds (Avalon, Cape

Shore, and Mt. Peyton), moderate sized herds (Grey River, Gaff Topsails, Pot Hill, and St. Anthony), and relatively large herds (Middle Ridge and La Poile). Group size data are inherently right-skewed with a large number of small groups and a small number of large groups, so for all models I compared generalized linear models parameterized with Poisson and negative binomial distributions using AIC model selection procedures (Tables S5.2, S5.3, & S5.4). In all cases, models parameterized with negative binomial distribution was selected and I report Nagelkerke's pseudo R^2 (Lefcheck 2016).

To meet the assumptions of normality, population density was log-transformed for all analyses. To test my first prediction, which was that average group size will increase as a function of increasing population density (P1), I included average group size for each herd-year combination as the response variable and log-transformed population density, herd, and year as fixed effects in the global model and compared this model to a model without herd or year (Table S5.2). To test my second and third predictions, which examined the relationship between group size and population density as a function of habitat type (P1b) and season (P1c), I included group size for each herd-year combination as the response variable and herd, year, and interactions between habitat type or season and log-transformed population density as fixed effects in the global model and compared this model to models without herd or year (Table S5.3). To test my fourth and fifth predictions, which examined the relationship between group size and habitat type (P2a) and season (P2b) independent of population density, I included year and an interaction between habitat type and season as main effects in the model and compared this model to a model without year (Table S5.4). All statistical analyses were conducted in R (R Core Team 2019).

5.4 Results

5.4.1 Group size and herd-level population density

In total, 10,272 groups from nine Newfoundland caribou herds were observed during aerial surveys between 1987–2013 (Table S5.1). In contrast to my prediction (P1a), average and typical annual group size decreased as a function of increasing population density (Figure 5.2). The negative relationship between average and typical annual group size and population density was significant for relatively smaller and larger herds, while this relationship was not significant for moderate sized herds (Figure 5.1; Table 5.1).

5.4.2 Group size, habitat, and season dependent on population density

For the nine Newfoundland caribou herds (Table 5.1), spatial locations for 566 groups were recorded between 2002–2011. Contrary to my predictions, group size did not vary between open (small herds: mean = 7.33, 95% CI: 4.86, 9.81; medium herds: mean = 9.39, 95% CI: 7.16, 11.63; large herds: mean = 11.45, 95% CI: 9.53, 13.37) or closed (small herds: mean = 8.40, 95% CI: 5.52, 11.27; medium herds: mean = 6.17, 95% CI: 4.15, 11.63; large herds: mean = 10.67, 95% CI: 7.90, 13.44) habitat types as a function of population density (P2b, Table 5.3; Figure 5.3a–c), while I observed a negative relationship between season (winter or calving) and population density (P2c, Table 5.3; Figure 5.3d–f). For small and moderate sized herds, group size was smaller during calving (small herds: mean = 6.97, 95% CI: 4.00, 9.95, moderate sized herds: mean = 7.07, 95% CI: 5.21, 8.94) than winter (small herds = 8.86, 95% CI: 6.85, 10.87, moderate sized herds: mean = 10.78, 95% CI: 7.34, 8.94). The negative relationship between group size and population density was more pronounced in calving than winter for small herds (Figure 5.3d) and more pronounced in winter than calving for moderate size herds (Figure 5.3e). By contrast, for relatively large herds, group size was smaller in winter (mean = 8.83, 95% CI:

7.14, 10.53) compared to calving (mean = 15.25, 95% CI: 12.26, 18.24), although this effect was near significant in the model (Table 5.3). The negative relationship between group size and population density was more pronounced in calving than winter (Figure 5.3f). In addition, group size varied by year as a function of changes in population density (Table 5.3).

5.4.3 Group size, habitat, and season independent of population density

For Fogo Island, spatial locations for 466 groups of caribou were recorded between 2016–2019. I found significant differences in group size between seasons (P2a), but not habitats (P2b), where on average, group size was larger in early winter compared to calving and summer, but there was no difference between open and closed habitats (Figure 5.4; Table 5.4). Specifically, I found that group sizes were largest in early winter for both open (mean = 8.5, 95% CI: 5.9, 11.2) and closed (mean = 5.3, 95% CI: 3.4, 7.3) habitats, moderate during calving for both open (mean = 2.9, 95% CI: 2.6, 3.2) and closed (mean = 2.5, 95% CI: 2.0, 3.0) habitats, and smallest in summer for both open (mean = 2.7, 95% CI: 1.3, 4.1) and closed (mean = 1.9, 95% CI: 1.3, 2.4) habitats (Figure 5.4).

5.5. Discussion

Animal groups on the landscapes vary in their size and number, and I examined how various ecological contexts influence group size in caribou. Specifically, group size for fission-fusion species is predicted to vary as a function of population density, habitat, and season (Jarman 1974; Gerard and Loisel 1995; Gerard et al. 2002), but the cumulative context dependency of these ecological factors is often omitted (Figure 5.1). Disentangling patterns of variation in group size and how these patterns may deviate from predictions, helps us infer costs and benefits of group behaviour. The null expectation based on the fission-fusion hypothesis for the relationship between group size and population density is a positive relationship, but, by contrast, I observed

a negative relationship between group size and population density. Further, I expected habitat would mediate group sizes because of the risk-reward trade-off typically associated with living in open compared to closed habitats, but I found limited evidence to support differences in group size across habitat types. For social ungulates, population density, habitat, and season are important ecological factors that influence group size and, at least for caribou these factors are rarely considered simultaneously.

In contrast to both optimal group size theory (Higashi and Yamamura 1993) and Caughley's (1964) hypothesis that group size for fission-fusion species should increase with population density (e.g. Pépin and Gerard 2008; Vander Wal et al. 2013b), I found that group size decreased as a function of population density. Woodland caribou in Newfoundland underwent drastic changes in population density in the early 2000s, where some herds declined in size by up to 95% (Table 5.2; Bastille-Rousseau et al. 2013). An alternative to Caughley's hypothesis is related to competition. Specifically, for caribou, population dynamics are regulated through density-dependent food competition (Mahoney et al. 2016; Schaefer et al. 2016). As density increases, and competition presumably increases, caribou could form smaller groups to reduce competition at high density. An alternative explanation is related to the rate and phase of population decline. Given that my comparison of group size across a declining population density, it could be that as populations declined, caribou were more sparsely distributed on the landscape and formed isolated, but larger, groups at low density. Importantly, my comparison of group size across a population density gradient occurred during a time when all herds were declining in size (Bastille-Rousseau et al. 2013). Prior studies which identified a positive relationship between group size and population density compared discrete sub-populations at a given time (e.g. Borkowski 2000) as opposed to a multi-year comparison during a decline. I posit

the state, i.e., growth phase, of the populations being compared is important for understanding group-size dynamics as it is for population dynamics. In addition, Caughley's hypothesis benefits from new insight about the potential for individual animals to make decisions about their social environment and group based on the benefits of group-living (Silk 2007).

Group size did not differ between open and closed habitat types for Newfoundland caribou herds (P1b) or for Fogo Island caribou (P2a). The primary explanation for larger group sizes in open areas is typically associated with improved sightlines for potential predators resulting in more effective vigilance and the ability to maintain a cohesive group (Creel et al. 2014), although there was no significant difference between group sizes in open and closed habitats. One explanation for similar sized groups in open and closed habitat types relates to the spatial distribution of open and closed habitats in the study areas. The spatial distribution for many other large herbivores, including kangaroos (*Macropus giganteus*), white-tailed and mule deer (*Odocoileus virginianus* and *O. hemionus*), and bison (*Bison bison*) are dominated primarily by plains or grassland ecosystems (Banks 2001; Lingle 2003; Fortin and Fortin 2009) that result in relatively homogeneous swaths of open habitat. By contrast, in the boreal forest, the distribution of open habitat types, including rocky outcrops, wetlands, and lichen barrens, heterogeneously distributed within the boreal forest matrix. Woodland caribou tend to select remote and heterogeneous areas within the boreal forest complex to avoid predators (Basille et al. 2015) and the lack of large swathes of open habitat in the boreal forest matrix could reduce the potential effect of habitat openness on group size. I therefore suggest the assumption that ungulate groups increase in size as a function of habitat openness needs to consider the heterogeneity of open habitats, for example, some species or populations live in homogenous environments, including regions dominated by grassland, meadow, or plains ecosystems. Habitat

availability This constitutes an important difference between tundra and woodland caribou, as group sizes for tundra herds are typically hundreds of individuals (Festa-Bianchet et al. 2011), while woodland caribou group sizes are much smaller (Table S5.1). My study contributes an alternative result to the broad literature highlighting the relationship between group size and habitat openness in ungulates (e.g. Borkowski 2000; Gerard et al. 2002; Barja and Rosellini 2008) and the more recent literature highlighting the role of habitat configuration as a potential driver of social processes (Webber and Vander Wal 2018; He et al. 2019).

We found that groups were larger in winter than summer or calving for most Newfoundland herds (P1c, but see below) and for Fogo Island caribou (P2b). Seasonal changes in group size for ungulates is related to the trade-off between the availability of foraging opportunities and coyote predation risk on Fogo Island (Ruckstuhl and Festa-Bianchet 2001). For other populations of caribou, group size was larger in winter than summer (Rettie and Messier 1998), and winters with deep snow tend to have larger groups than winters with shallow snow (Jung et al. 2019).The conspecific attraction hypothesis (Fletcher 2009) posits that social animals obtain cues about foraging opportunities from conspecifics by changing the degree to which they associate and form social groups when the availability of foraging resources are limited (Peignier et al. 2019). For caribou, foraging resources are limited and often of lower quality in winter (Brown and Theberge 1990; Ferguson et al. 2001; Beumer et al. 2017), and my observation that group size was larger in winter than summer and calving supports the idea proposed elsewhere that caribou tend to aggregate in winter to share, or take advantage of, social information about foraging opportunities (Peignier et al. 2019). Similarly, in white-tailed and mule deer (Lingle 2003), elk (Vander Wal et al. 2013b), and bison (Fortin and Fortin 2009) average group size was larger in winter, a pattern across ungulates which appears to be linked to social information

transfer (Merkle et al. 2015). In summer, ungulate group sizes are consistently smaller, presumably because of the abundance of forage. The Middle Ridge and La Poile herds are a notable exception regarding seasonality of group size. Group size was larger during calving than winter because caribou in these herds aggregate on calving grounds (Rayl et al. 2014), while other herds do not. Approximately 80% of animals in the Middle Ridge herd aggregate on the calving ground to reduce predation risk via a detection-dilution trade-off (Fifield et al. 2012; Bonar et al. 2020). As a result, the number of animals in a relatively small area temporarily increases during calving, such that group sizes were twice as large during calving compared to winter. My findings, in combination with those from past studies, suggest that group sizes for ungulates almost always vary seasonally due to temporal variation in the availability of foraging resources (Lagory 1986; Fryxell 1991; Gerard and Loisel 1995; Borkowski 2000; Lingle 2003; Fortin et al. 2009).

While my study spans multiple decades and presents long-term data presents strong inference into broad trends, I also wish to acknowledge the caveats associated with my data and analytical approach. Specifically, wildlife management agencies typically only survey ungulates, including caribou, during winter and calving (e.g. Heard and Ouellet 1994; Hegel et al. 2012). In the case of the Newfoundland and Labrador Wildlife Division, caribou herd composition surveys occurred three times annually: during calving, autumn, and winter (Mahoney and Weir 2010). As a result, I was unable to directly compare winter and summer group sizes for the Newfoundland herds; although I did compare group sizes between calving, summer, and winter for caribou on Fogo Island. Finally, a common criticism of studies measuring group size in ungulates is that groups in forests may be under-estimated due differential detection by observers in open compared to closed habitats (Vander Wal et al. 2011). In a recent study, I examined differences

in social network measures of GPS collared caribou across different habitat types and found support for the expectation that social groups were larger in open habitats compared to closed habitats (Robitaille et al. 2020). Importantly, my measures of social groups based on GPS collars are continuous and biases in detection are not an assumption of these analyses. Taken together, these past results, in combination with my results on group size across habitat type, suggest that group sizes in open habitats may have been under-estimated. I therefore cautiously interpret out finding that groups did not differ in size between habitat types and encourage future studies to use a more precise measure of habitat type to overcome the potential for bias associated with counting groups in open or closed habitats.

Animals assume the benefits of grouping to maximize fitness and I show that average group size depends on context, including population density, habitat, and season. The cumulative effect of different contexts on variation in group size could influence the ecological, and potentially evolutionary, causes and consequences of group living. For example, different ecological contexts can influence the ability for individuals in a group to communicate as well as the spatial arrangement of group members (Lima 1995; Dostie et al. 2016). Communication and spatial arrangement represent behavioural mechanisms that facilitate the proximate benefits of group-living, while ultimately, these benefits ensure group members maximize fitness according to the ecological context. For caribou, I observed that average group size varies across a gradient of population density and across seasons. Importantly, as caribou populations decline throughout their range (Vors and Boyce 2009; Mallory and Boyce 2017), I highlight an unexpected outcome in that group size could increase with decreasing population density. The effects of drastic declines in population density can affect a variety of life-history, morphological, and behavioural traits. Increased group size at low population density could elicit Alle effects, which are

instances vital rates, i.e. survival and reproduction, increase at very low population density (Stephens and Sutherland 1999). For social animals like caribou, Allee effects could improve vital rates and reduce the likelihood a population is extirpated (Angulo et al. 2017). Given the potential importance of social behaviour from a conservation and management perspective (Blumstein 2010; Snijders et al. 2017), future work should assess how various conservation threats, including anthropogenic disturbance of critical habitat, influences patterns of grouping and whether a potential disruption to social cohesion influences population vital rates and Allee effects.

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Table 5.1: Summary of herd surveys as well as mean group size data for nine caribou herds in Newfoundland during the peak (1987–1997) and decline phases (2001–2013).

Herd	Peak (1987-1997)				Decline (2001-2013)			
	Number of surveys	Number of groups observed	Mean herd size (95% CI)	Mean group size (95% CI)	Number of surveys	Number of groups observed	Mean herd size (95% CI)	Mean group size (95% CI)
Avalon	2	125	6,856 (3,711, 10,001)	8.04 (7.0, 9.08)	10	276	548 (382, 816)	6.66 (5.81, 7.52)
Cape shore	4	296	1,077 (968, 1,186)	5.59 (5.0, 6.17)	8	362	392 (300, 484)	6.27 (5.21, 7.33)
Gaff Topsails	3	278	4,684 (4,147, 5,220)	6.41 (5.59, 7.24)	11	825	2,262 (1,882, 2,643)	8.66 (7.88, 9.42)
Grey River	3	424	11,004 (10,725, 11,282)	5.83 (5.11, 6.55)	9	271	2,551 (1,242, 3,861)	4.42 (3.75, 5.07)
Lapoile	8	854	10,220 (9,577, 10,864)	9.98 (9.26, 10.71)	11	838	4,925 (4,190, 5,659)	9.69 (8.86, 10.51)
Middle Ridge	6	1,519	18,135 (16,673, 19,596)	5.78 (5.48, 6.08)	13	1,862	11,082 (9,373, 12,792)	10.36 (9.82, 10.91)
Mt. Peyton	3	180	1,676 (1,462, 1,889)	8.31 (6.84, 9.78)	11	505	758 (648, 868)	5.21 (4.48, 5.95)
Pothill	3	225	4,872 (4,397, 5,346)	7.87 (6.83, 8.91)	11	1,049	2,925 (2,370, 3,479)	5.79 (5.26, 6.33)
St. Anthony	1	67	7,318	9.77 (8.33, 11.2)	10	316	3,164 (2,225, 4,102)	5.77 (5.10, 6.43)
Totals/means	33	3,968	–	7.09 (6.84, 7.34)	94	6,304	–	7.99 (7.73, 8.26)

Table 5.2: Summary of three generalized linear models parameterized with negative binomial distributions testing for effects of log-transformed population density on annual average group size for nine Newfoundland caribou herds between 2001–2013. Analyses were separated based on herd size such that small herds (Avalon, Cape Shore, and Mt. Peyton), moderate sized herds (Grey River, Gaff Topsails, Pot Hill, and St. Anthony), and relatively large caribou herds (Middle Ridge and Lapoile) were grouped together (model selection results available in Table S5.2).

Model	**Coefficient ± se[1]**	**z-value**	**p-value**
Small herds (pseudo R^2 = 0.19)			
Intercept	3.64 ± 0.71	5.15	**<0.001**
log(density)	–0.23 ± 0.11	–2.18	**0.03**
Medium herds (pseudo R^2 = 0.03)			
Intercept	3.08 ±1.02	3.02	**0.003**
log(density)	–0.12 ± 0.13	–0.98	0.32
Large herds (pseudo R^2 = 0.39)			
Intercept	7.41 ± 1.38	5.36	**<0.001**
log(density)	–0.55 ± 0.15	–3.56	**0.0003**

Table 5.3: Summary of three generalized linear models parameterized with negative binomial distributions estimating the effects of habitat type, season, and log-transformed population density on group size across for nine Newfoundland caribou herds. Analyses were separated based on herd size such that small herds (Avalon, Cape Shore, and Mt. Peyton), moderate sized herds (Grey River, Gaff Topsails, Pot Hill, and St. Anthony), and relatively large caribou herds (Middle Ridge and Lapoile) were grouped together (model selection results available in Table S5.3).

Fixed effects	**Coefficient ± se**	**z-value**	**p- value**
Small herds (pseudo R^2 = 0.31)			
Intercept	–41.96 ± 15.1	–2.78	**0.005**
log(density)	3.61 ± 4.77	2.89	**0.004**
Habitat type(open)[1]	6.32 ± 2.18	0.76	0.45
Season (winter)[2]	54.78 ± 18.1	3.03	**0.002**
Year[3]			
2004	1.10 ± 1.06	1.04	0.30
2005	2.21 ± 0.58	3.79	**0.0001**
2006	2.77 ± 0.75	3.71	**0.0002**
Habitat type(open) x log(density)	–0.57 ± 0.72	–0.79	0.42
Season (winter) x log(density)	–8.13 ± 2.78	–2.92	**0.003**
Medium herds (pseudo R^2 = 0.51)			
Intercept	–25.16 ± 9.67	–2.61	**0.009**
log(density)	–2.50 ± 6.57	–0.38	**0.003**
Habitat type(open)[1]	3.57 ± 1.20	2.97	0.70
Season (winter)[2]	57.38 ± 13.27	4.32	**<0.0001**
Year[4]			
2003	–0.84 ± 0.46	–1.84	0.07
2004	–2.83 ± 0.65	–4.34	**<0.0001**
2005	–2.07 ± 0.55	–3.79	**0.0001**
2006	–0.68 ± 0.56	–1.23	0.22
2008	0.16 ± 0.75	0.21	0.83
2010	–1.57 ± 1.22	–1.28	0.20
2011	–0.81 ± 0.86	–0.94	0.35
Habitat type(open) x log(density)	0.33 ± 0.81	0.42	0.67
Season (winter) x log(density)	–7.16 ± 1.64	–4.36	**<0.0001**
Large herds (pseudo R^2 = 0.45)			
Intercept	10.3 ± 3.89	2.64	**0.008**
log(density)	–0.95 ± 0.44	–2.15	**0.03**

Habitat type(open)[1]	2.93 ± 2.65	1.11	0.27
Season (winter)[2]	–7.14 ± 4.24	–1.68	0.09
Year[4]			
2004	1.15 ± 0.44	2.64	**0.008**
2006	1.04 ± 0.129	3.53	**0.0004**
2007	0.14 ± 0.54	0.25	0.80
2010	0.74 ± 0.25	2.95	**0.003**
2011	0.90 ± 0.35	2.58	**0.01**
Habitat type(open) x log(density)	–0.32 ± 0.28	–1.14	0.26
Season (winter) x log(density)	0.82 ± 0.48	1.69	0.09

[1]reference category is closed habitat; [2]reference category is calving; [3]reference category is 2003; [4]reference category is 2002.

Table 5.4: Summary of generalized linear model parameterized with a negative binomial distribution estimating effects of habitat type (open or closed) and season (calving, summer, and early winter) for the Fogo Island caribou herd (model selection results presented in Table S5.4).

Fixed effects	**Coefficient ± se[1]**	**z-value**	**p-value**
Intercept	0.93 ± 0.10	9.61	**<0.001**
Habitat type (open)	0.14 ± 0.11	1.20	0.23
Season (early winter)	0.74 ± 0.21	3.56	**0.0003**
Season (summer)	–0.31 ± 0.20	–1.51	0.13
Habitat type x season			
-Open x early winter	0.33 ± 0.24	1.40	0.16
-Open x summer	0.23 ± 0.27	0.82	0.41

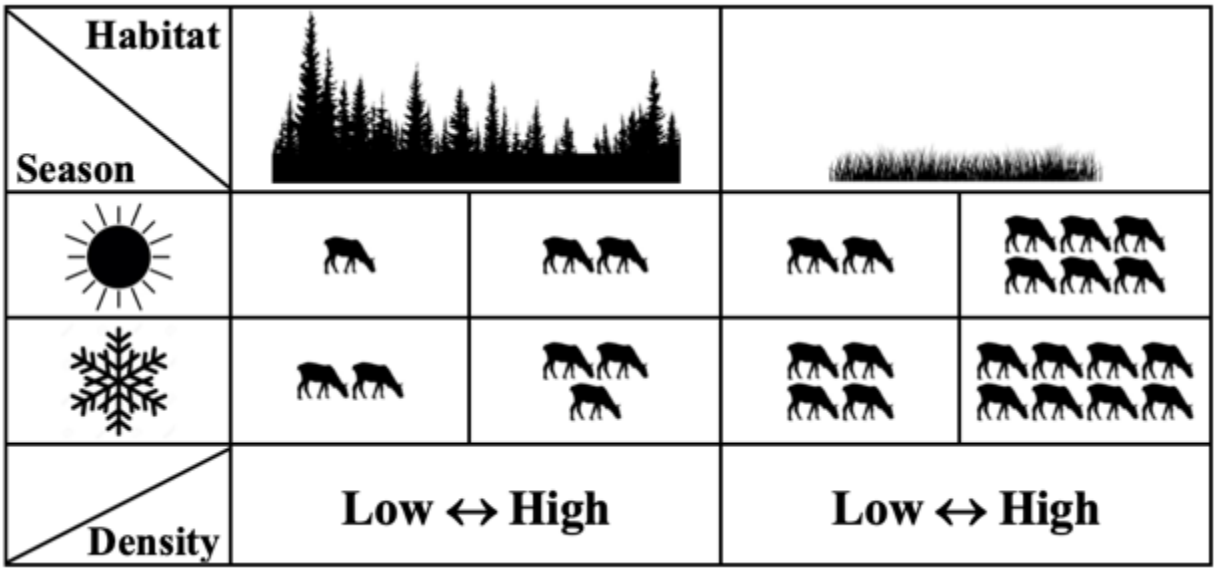

Figure 5.1: Conceptual demonstration of how caribou group size is predicted to vary as a function of habitat (closed or open habitats), season (summer or winter), and population density (ranging from low to high). The number of caribou in each panel represents the predicted *relative* group size for a given combination of variables compared to another combination of variables. For example, group size in closed habitats during the summer is predicted to be lower than group size in open habitats in summer (independent of density).

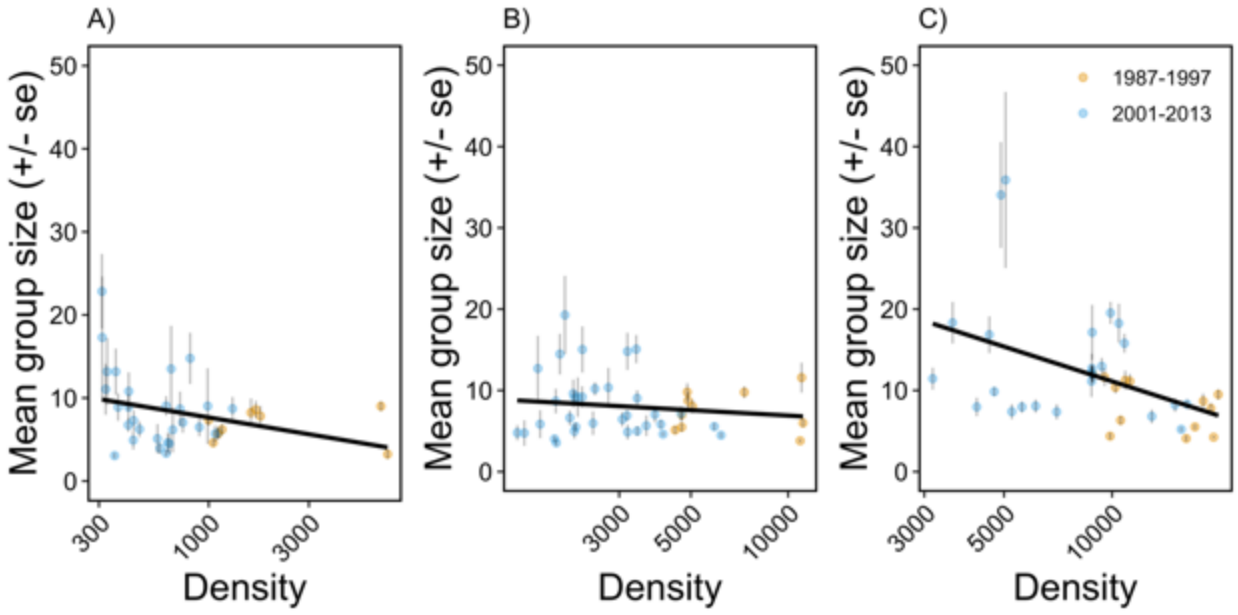

Figure 5.2: Annual average group size as a function of population density (log-scale) for A) small herds (Avalon, Cape Shore, and Mt. Peyton), B) moderate sized herds (Grey River, Gaff Topsails, Pot Hill, and St. Anthony), and C) relatively large caribou herds (Middle Ridge and Lapoile). Note, population density was log-transformed for analyses but untransformed values are presented and mean group size was calculated during two distinct time periods: the peak phase of population density (orange dots) and the decline phase (blue dots). Vertical grey lines represent standard error for each annual average group size (see Table 5.2).

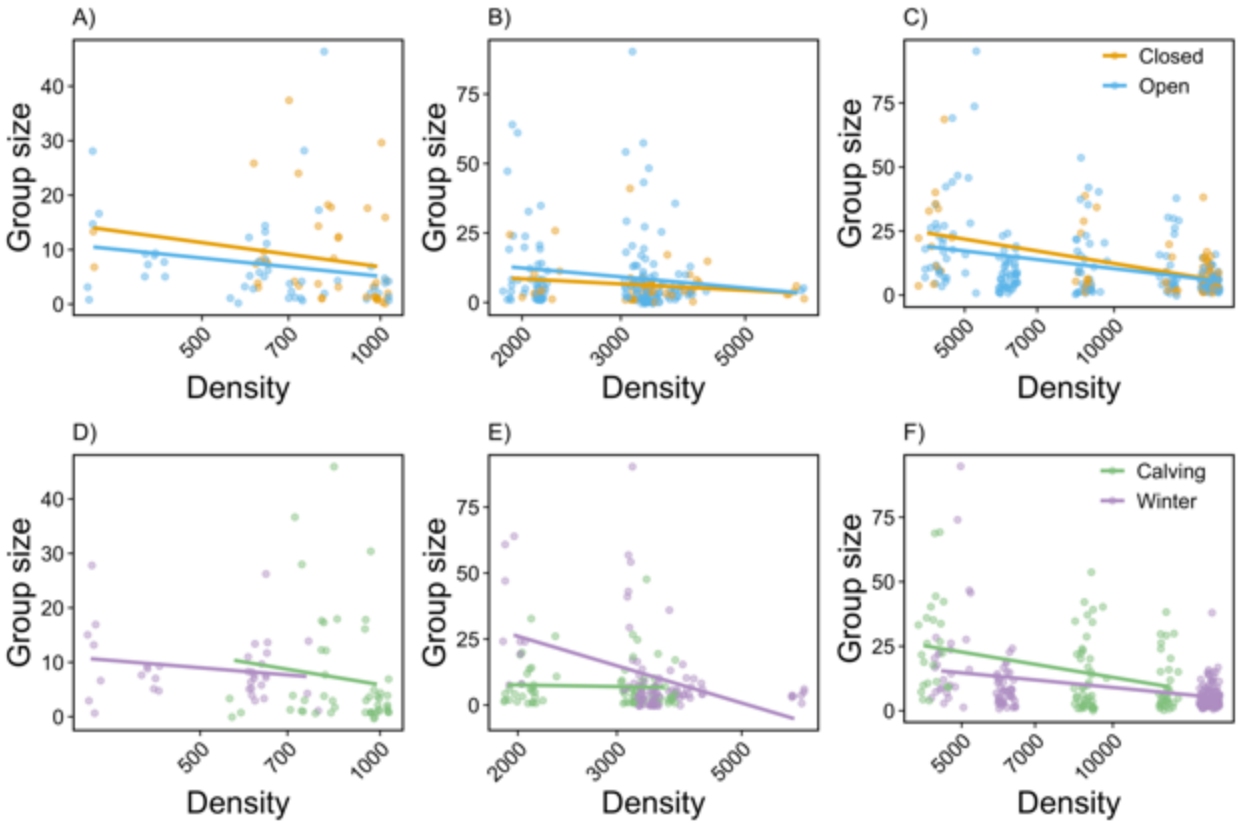

Figure 5.3: Relationship between group size and population density (log-scale) as a function of habitat type (panels A–C) and season (panels D–F) for nine caribou herds in Newfoundland between 2001–2013. Panels A & D are small herds (Avalon, Cape Shore, and Mt. Peyton), panels B & E are moderate sized herds (Grey River, Gaff Topsails, Pot Hill, and St. Anthony), and panels C & F are relatively large herds (Middle Ridge and Lapoile). Population density was log-transformed for analyses but untransformed values are presented and the interaction between log-transformed density and habitat type was non-significant for all herds, while the interaction between log-transformed density and season was significant for small and moderate, but not large, herds (Table 5.4). Note, clustering along the x-axis represents different herd-year combinations of data.

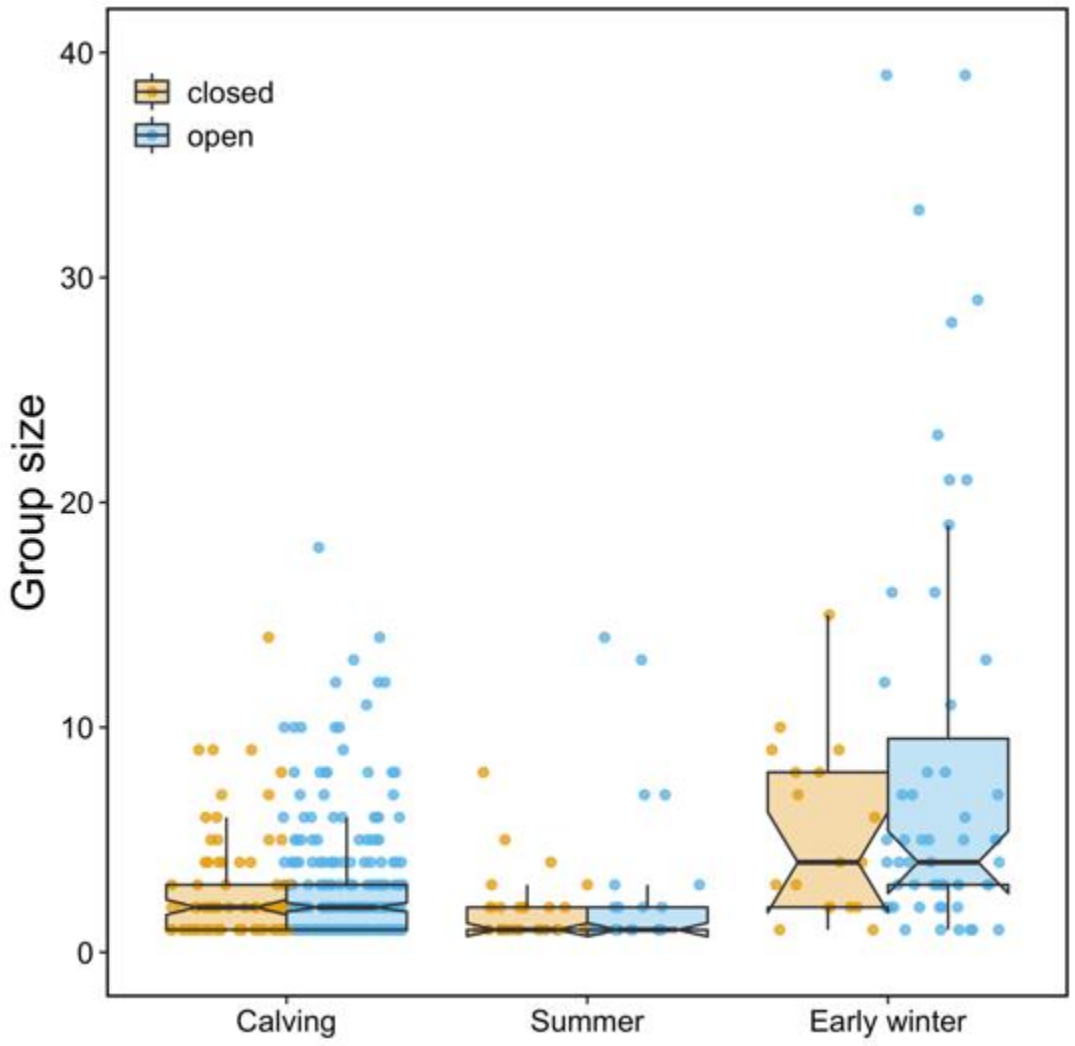

Figure 5.4: Comparison of group size across habitat types (open or closed) and seasons for the Fogo Island caribou herd (2016–2019). Note, early winter group sizes were larger in both open and closed habitats than calving and summer and there was no difference between habitat types within seasons. Points show the distribution of data, thick dark lines represent the median, upper and lower edges of each box represent the interquartile range (25% and 75% of data), notches represent the differences in each season, and whiskers represent the upper and lower quantiles (2.5% and 97.5% of data).

5.7 References

Alexander RD. 1974. The evolution of social behavior. Annu Rev Ecol Evol Syst. 5:325–383.

Barja I, Rosellini S. 2008. Does habitat type modify group size in roe deer and red deer under predation risk by Iberian wolves? Can J Zool. 86(3):170–176. doi:10.1139/Z07-129.

Barten NL, Bowyer RT, Jenkins KJ. 2001. Habitat use by female caribou: Tradeoffs associated with parturition. J Wildl Manage. 65(1):77–92.

Basille M, Fortin D, Dussault C, Bastille-Rousseau G, Ouellet JP, Courtois R. 2015. Plastic response of fearful prey to the spatiotemporal dynamics of predator distribution. Ecology. 96(10):2622–2631. doi:10.1890/14-1706.1.

Bastille-Rousseau G, Schaefer JA, Lewis KP, Mumma MA, Ellington EH, Rayl ND, Mahoney SP, Pouliot D, Murray DL. 2016. Phase-dependent climate-predator interactions explain three decades of variation in neonatal caribou survival. J Anim Ecol. 85(2):445–456. doi:10.1111/1365-2656.12466.

Bastille-Rousseau G, Schaefer JA, Mahoney SP, Murray DL. 2013. Population decline in semi-migratory caribou (*Rangifer tarandus*): intrinsic or extrinsic drivers? Can J Zool. 91(11):820–828. doi:doi:10.1139/cjz-2013-0154.

Bergerud AT. 1974. Relative abundance of food in winter for Newfoundland caribou. Oikos. 25(3):379–387.

Bergerud AT, Mercer WE. 1989. Caribou introductions in eastern North America. Wildl Soc Bull. 17(2):111–120.

Beumer LT, Varpe O, Hansen BB. 2017. Cratering behaviour and faecal C:N ratio in relation to seasonal snowpack characteristics in a High-Arctic ungulate. Polar Res. 36(1):1286121. doi:10.1080/17518369.2017.1286121.

Body G, Weladji RB, Holand O, Nieminen M. 2015. Fission-fusion group dynamics in reindeer reveal an increase of cohesiveness at the beginning of the peak rut. Acta Ethol. 18(2):101–110. doi:10.1007/s10211-014-0190-8.

Body G, Weladji RB, Holand Ø, Nieminen M. 2014. Highly competitive reindeer males control female behavior during the rut. PLoS One. 9(4):e95618. doi:10.1371/journal.pone.0095618.

Bonar M, Ellington EH, Lewis KP, Vander Wal E. 2018. Implementing a novel movement-based approach to inferring parturition and neonate calf survival. PLoS One. 13:e0192204.

Bonar M, Lewis K, Webber QMR, Dobbin M, Laforge MP, Vander Wal E. 2020. Geometry of the ideal free distribution: individual behavioural variation and annual reproductive success in aggregations of a social ungulate. Ecol Lett. 23:1360–1369. doi:10.1111/ele.13563.

Borkowski J. 2000. Influence of the density of a sika deer population on activity, habitat use, and group size. Can J Zool. 78(8):1369–1374. doi:10.1139/z00-071.

Brennan A, Cross PC, Creel S. 2015. Managing more than the mean: using quantile regression to identify factors related to large elk groups. J Appl Ecol. 52:1656–1664. doi:10.1111/1365-2664.12514.

Brown WK, Theberge JB. 1990. The Effect of Extreme Snowcover on Feeding-Site Selection by Woodland Caribou. J Wildl Manage. 54(1):161–168.

Caughley G. 1964. Social Organization and Daily Activity of the Red Kangaroo and the Grey Kangaroo. J Mammal. 45(3):429–436.

Christianson DA, Creel S. 2007. A review of environmental factors affecting elk winter diets. J Wildl Manage. 71(1):164–176.

Creel S, Schuette P, Christianson D. 2014. Effects of predation risk on group size, vigilance, and foraging behavior in an African ungulate community. Behav Ecol. 25(4):773–784. doi:10.1093/beheco/aru050.

Djaković N, Holand O, Hovland AL, Weladji RB, Røed KH, Nieminen M. 2015. Effects of males presence on female behaviour during the rut. Ethol Ecol Evol. 27(2):148–160. doi:10.1080/03949370.2014.905498.

Dostie MJ, Lusseau D, Bonnell T, Clarke PMR, Chaplin G, Kienzle S, Barrett L, Henzi SP. 2016. Proof of principle: the adaptive geometry of social foragers. Anim Behav. 119:173–178. doi:10.1016/j.anbehav.2016.07.011.

Duquette LS, Klein DR. 1987. Activity budgets and group size of caribou during spring migration. Can Jounal Zool. 65(164–168).

Ferguson MAD, Gauthier L, Messier F. 2001. Range shift and winter foraging ecology of a population of Arctic tundra caribou. Can J Zool. 79(5):746–758. doi:10.1139/cjz-79-5-746.

Festa-Bianchet M, Ray JC, Boutin S, Côté SD, Gunn A. 2011. Conservation of caribou (*Rangifer tarandus*) in Canada: an uncertain future. Can Jounal Zool. 434:419–434. doi:10.1139/Z11-025.

Fifield DA, Lewis KP, Gullage SE. 2012. Application of distance sampling to determine calving ground abundance and aggregation of parturient females in the Middle Ridge herd, June 2012. Tech Bull No 005, Sustain Dev Strateg Sci Gov Newfoundl Labrador, St John's, NL.

Fletcher RJ. 2009. Does attraction to conspecifics explain the patch-size effect? An experimental test. Oikos. 118(8):1139–1147. doi:10.1111/j.1600-0706.2009.17342.x.

Fortin D, Fortin ME. 2009. Group-size-dependent association between food profitability, predation risk and distribution of free-ranging bison. Anim Behav. 78(4):887–892.

doi:10.1016/j.anbehav.2009.06.026.

Fryxell JM. 1991. Forage quality and aggregation by large herbivores. Am Nat. 138(2):478–498.

Gerard JF, Bideau E, Maublanc ML, Loisel P, Marchal C. 2002. Herd size in large herbivores: Encoded in the individual or emergent? Biol Bull. 202(3):275–282.

Hamilton WD. 1964. The genetical evolution of social behaviour. II. J Theor Biol. 7(1):17–52. doi:10.1016/0022-5193(64)90039-6.

He P, Maldonado-Chaparro AA, Farine DR. 2019. The role of habitat configuration in shaping social structure: a gap in studies of animal social complexity. Behav Ecol Sociobiol. 73:9.

Heard DC, Ouellet JP. 1994. Dynamics of an introduced caribou population. Arctic. 47(1):88–95. doi:10.14430/arctic1276.

Hegel TM, Russell K, Jung TS. 2012. Using temporary dye marks to estimate ungulate population abundance in southwest Yukon, Canada. Rangifer. 20:219–226. doi:10.7557/2.32.2.2271.

Higashi M, Yamamura N. 1993. What determines animal group size? Insider-outsider conflict and its resolution. Am Nat. 142(3):553–563.

Jarman PJ. 1974. The social organisation of antelope in relation to their ecology. Behaviour. 48(3):215–267.

Jung TS, Larter NC, Allaire DG. 2019. Social organization of boreal woodland caribou (*Rangifer tarandus caribou*) in response to decreasing annual snow depth. Mammal Res. 64:377–385.

Kasozi H, Montgomery RA. 2020. Variability in the estimation of ungulate group sizes complicates ecological inference. Ecol Evol.(May):1–9. doi:10.1002/ece3.6463.

Krause J, Ruxton GD. 2002. Living in groups. Oxford University Press.

L'Italien L, Weladji RB, Holand Ø, Røed KH, Nieminen M, Côté SD. 2012. Mating group size and stability in reindeer *Rangifer tarandus*: The effects of male characteristics, sex ratio and male age structure. Ethology. 118(8):783–792. doi:10.1111/j.1439-0310.2012.02073.x.

Lardy S, Allainé D, Bonenfant C, Cohas A. 2015. Sex-specific determinants of fitness in a social mammal. Ecology. 96(11):2947–2959.

Lefcheck JS. 2016. piecewiseSEM: Piecewise structural equation modelling in r for ecology, evolution, and systematics. Methods Ecol Evol. 7(5):573–579. doi:10.1111/2041-210X.12512.

Lesmerises F, Johnson CJ, St-Laurent M-H. 2018. Landscape knowledge is an important driver of the fission dynamics of an alpine ungulate. Anim Behav. 140:39–47.

doi:10.1016/j.anbehav.2018.03.014.

Lewis KP, Mahoney SP. 2014. Caribou survival, fate, and cause of mortality in Newfoundland: a summary and analysis of the patterns and causes of caribou survival and mortality in Newfoundland during a period of rapid population decline (2003-2012). Tech Bull No 009, Sustain Dev Strateg Sci Gov Newfoundl Labrador, St John's, NL.

Lima SL. 1995. Back to the basics of anti-predatory vigilance: the group-size effect. Anim Behav. 49:11–20.

Lima SL, Dill LM. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. Can J Zool. 68(4):619–640. doi:10.1139/z90-092.

Lingle S. 2003. Group composition and cohesion in sympatric white-tailed deer and mule deer. Can J Zool. 81(7):1119–1130. doi:10.1139/z03-097.

Mahoney SP, Lewis KP, Weir JN, Morrison SF, Luther GJ, Schaefer JA, Pouliot D, Latifovic R. 2016. Woodland caribou calf mortality in Newfoundland: insights into the role of climate, predation and population density over three decades of study. Popul Ecol. 58(1):91–103. doi:10.1007/s10144-015-0525-y.

Mahoney SP, Virgl JA. 2003. Habitat selection and demography of a nonmigratory woodland caribou population in Newfoundland. Can J Zool. 81(2):321–334. doi:10.1139/z02-239.

Mahoney SP, Virgl JA, Fong DW, MacCharles AM, McGrath M. 1998. Evaluation of a Mark-Resighting Technique for Woodland Caribou in Newfoundland. J Wildl Manage. 62(4):1227–1235.

Mahoney SP, Weir JN. 2010. Caribou data synthesis - progress report. Overview of the status of woodland caribou in insular Newfoundland: research methodology, results, interpretations and future projects. (001).

Mallory CD, Boyce MS. 2017. Observed and predicted effects of climate change on Arctic caribou and reindeer. Environ Rev. 13(June):1–13.

Mathisen JH, Landa A, Andersen R, Fox JL. 2003. Sex-specific differences in reindeer calf behavior and predation vulnerability. Behav Ecol. 14(1):10–15. doi:10.1093/beheco/14.1.10.

McLellan BN, Serrouya R, Wittmer HU, Boutin S. 2010. Predator-mediated Allee effects in multi-prey systems. Ecology. 91(1):286–292.

McLoughlin PD, Gaillard J-M, Boyce MS, Bonenfant C, Messier F, Duncan P, Delorme D, Van Moorter B, Said S, Klein F. 2007. Lifetime reproductive success and composition of the home range in a large herbivore. Ecology. 88(12):3192–3201.

McNamara JM, Houston AI. 1992. Evolutionarily stable levels of vigilance as a function of

group size. Anim Behav. 43(4):641–658. doi:10.1016/S0003-3472(05)81023-1.

Merkle JA, Sigaud M, Fortin D. 2015. To follow or not? How animals in fusion-fission societies handle conflicting information during group decision-making. Ecol Lett. 18(8):799–806. doi:10.1111/ele.12457.

Morrison SF, Weir JN, Mahoney SP, Luther JG. 2012. Projection of woodland caribou populations in Newfoundland: An application of Leslie - Matrix populaton models to predict future of Newfoundland caribou herds (2010-2035). St. John's, NL, Canada.

Muller Z, Cuthill IC, Harris S. 2018. Group sizes of giraffes in Kenya: the influence of habitat , predation and the age and sex of individuals. J Zool.:1–11. doi:10.1111/jzo.12571.

Peignier M, Webber QMR, Koen EL, Laforge MP, Robitaille AL, Vander Wal E. 2019. Space use and social association in a gregarious ungulate: Testing the conspecific attraction and resource dispersion hypotheses. Ecol Evol. 9:5133–5145. doi:10.1002/ece3.5071.

Pépin D, Gerard J-F. 2008. Group dynamics and local population density dependence of group size in the Pyrenean chamois, *Rupicapra pyrenaica*. Anim Behav. 75(2):361–369. doi:10.1016/j.anbehav.2006.09.030.

R Core Team. 2019. R: A language and environment for statistical computing. :https://www.r-project.org/.

Rayl ND, Fuller TK, Organ JF, McDonald JE, Mahoney SP, Soulliere C, Gullage SE, Hodder T, Norman F, Porter T, et al. 2014. Mapping the distribution of a prey resource: neonate caribou in Newfoundland. J Mammal. 95(2):328–339. doi:10.1644/13-MAMM-A-133.1.

Reimers E, Lund S, Ergon T. 2011. Vigilance and fright behaviour in the insular Svalbard reindeer (*Rangifer tarandus platyrhynchus*). Can J Zool. 89(8):753–764. doi:10.1139/z11-040.

Reimers E, Miller FL, Eftestøl S, Colman JE, Dahle B. 2006. Flight by feral reindeer Rangifer tarandus tarandus in response to a directly approaching human on foot or on skis. Wildlife Biol. 12(4):403–413. doi:10.2981/0909-6396(2006)12[403:fbfrrt]2.0.co;2.

Reimers E, Røed KH, Colman JE. 2012. Persistence of vigilance and flight response behaviour in wild reindeer with varying domestic ancestry. J Evol Biol. 25(8):1543–1554. doi:10.1111/j.1420-9101.2012.02538.x.

Rettie WJ, Messier F. 1998. Dynamics of woodland caribou populations at the southern limit of their range in Saskatchewan. Can J Zool. 76(2):251–259. doi:10.1139/z97-193.

Ruckstuhl KE, Festa-Bianchet M. 2001. Group choice by subadult bighorn rams: trade-offs between foraging efficiency and predator avoidance. Ethology. 107(2):161–172. doi:10.1046/j.1439-0310.2001.00663.x.

Schaefer JA, Mahoney SP. 2013. Spatial dynamics of the rise and fall of caribou (*Rangifer tarandus*) in Newfoundland. Can J Zool. 91(11):767–774. doi:10.1139/cjz-2013-0132.

Schaefer JA, Mahoney SP, Weir JN, Luther JG, Soulliere CE. 2016. Decades of habitat use reveal food limitation of Newfoundland caribou. J Mammal. 97(2):386–393. doi:10.1093/jmammal/gyv184.

Silk JB. 2007. The adaptive value of sociality in mammalian groups. Philos Trans R Soc B. 362(1480):539–559. doi:10.1098/rstb.2006.1994.

Snijders L, Blumstein DT, Stanley CR, Franks DW. 2017. Animal social network theory can help wildlife conservation. Trends Ecol Evol. 32(8):567–577. doi:10.1016/j.tree.2017.05.005.

Stamps JA. 1988. Conspecific attraction and aggregation in territorial species. Am Nat. 131(3):329–347.

Stuart-Smith AK, Bradshaw CJA, Boutin S, Hebert DM, Rippin AB. 1997. Woodland caribou relative to landscape patterns in northeastern Alberta. J Wildl Manage. 61(3):622–633.

Taillon J, Festa-Bianchet M, Côté SD. 2012. Shifting targets in the tundra: Protection of migratory caribou calving grounds must account for spatial changes over time. Biol Conserv. 147(1):163–173. doi:10.1016/j.biocon.2011.12.027.

Tennenhouse EM, Weladji RB, Holand O, Roed KH, Nieminen M. 2011. Mating group composition influences somatic costs and activity in rutting dominant male reindeer (*Rangifer tarandus*). Behav Ecol Sociobiol. 65(2):287–295. doi:10.1007/s00265-01.

Uccheddu S, Body G, Weladji RB, Holand O, Nieminen M. 2015. Foraging competition in larger groups overrides harassment avoidance benefits in female reindeer (*Rangifer tarandus*). Oecologia. 179:711–718.

Vors LS, Boyce MS. 2009. Global declines of caribou and reindeer. Glob Chang Biol. 15(11):2626–2633. doi:10.1111/j.1365-2486.2009.01974.x.

Vander Wal E, van Beest FM, Brook RK. 2013. Density-dependent effects on group size are sex-specific in a gregarious ungulate. PLoS One. 8(1):e53777. doi:10.1371/journal.pone.0053777.

Vander Wal E, Mcloughlin PD, Brook RK. 2011. Spatial and Temporal Factors Influencing Sightability of Elk. J Wildl Manage. 75(6):1521–1526. doi:10.1002/jwmg.208.

Vander Wal E, Paquet PC, Messier F, Mcloughlin PD. 2013. Effects of phenology and sex on social proximity in a gregarious ungulate. Can J Zool. 609(October 2012):601–609. doi:10.1139/cjz-2012-0237.

Webber QMR, Vander Wal E. 2018. An evolutionary framework outlining the integration of individual social and spatial ecology. J Anim Ecol. 87:113–127. doi:10.1111/1365-2656.12773.

Weckerly FW, Ricca MA, Giguere N. 2014. Aggression and Coexistence in Female Caribou. Arctic. 67(2):189–195.

Weir JN, Mahoney SP, McLaren B, Ferguson SH. 2007. Effects of Mine Development on Woodland Caribou Rangifer Tarandus Distribution. Wildlife Biol. 13(1):66–74. doi:10.2981/0909-6396(2007)13[66:eomdow]2.0.co;2.

Williams CK, Lutz RS, Applegate RD. 2003. Optimal group size and northern bobwhite coveys. Anim Behav. 66(2):377–387. doi:10.1006/anbe.2003.2215.

CHAPTER 6:THE ADAPTIVE VALUE OF DENSITY-DEPENDENT HABITAT SPECIALIZATION AND SOCIAL NETWORK CENTRALITY

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6.1 Abstract

Density dependence is a fundamental ecological process. Patterns of animal habitat selection and social behaviour can be density-dependent and theory predicts that density-dependent traits should affect reproduction, survival, and therefore fitness and population dynamics. The Ideal Free Distribution and Optimal Foraging Theories present distinct predictions about how the effect of habitat selection on fitness differs across a population density gradient. Using a social ungulate (*Rangifer tarandus*) as a model system, I test competing hypotheses about how covariance in habitat specialization, social behaviour, and fitness vary across a population density gradient. Within the behavioural reaction norm framework, I estimated repeatability, plasticity, and phenotypic covariance among social behaviours and habitat selection to demonstrate the adaptive value of these phenotypes across a population density gradient. In support of Optimal Foraging Theory, but not the Ideal Free Distribution, I found that habitat specialists had higher fitness at high density, but were also less social than habitat generalists, suggesting the possibility that specialists were inhibited from being social. My findings illustrate that social strength and habitat specialization varied consistently among individuals across a density gradient, but that habitat specialists maximized fitness at high density. Taken together, my study provides preliminary support for Optimal Foraging Theory as the driving mechanism for density-dependent habitat specialization.

Key words: caribou, density dependence, Ideal Free Distribution, Optimal Foraging Theory, social network analysis, resource selection functions

6.2 Introduction

Our understanding of animal ecology can be simplified to incorporate five fundamental principles: organisms consume resources, require space to live, interact with members of the same and other species, live in dynamic environments, and copy their genes (Morris 2003). These principals extend directly to my understanding of density dependence in animal populations. Animals consume resources as they are available, but as population density increases, resources become limited and competition among conspecifics influences the ability of animals to use space, interact with conspecifics, and copy their genes. A particularly salient example integrating these principals is my ability to disentangle apparent social behaviour from shared preferences for habitats or resources and to assess the relative impacts of social behaviour and habitat selection on individual fitness parameters (i.e., survival and reproductive success; Webber and Vander Wal 2018). Patterns of habitat selection (i.e., the non-random use of available habitats; Morris 2003) may vary based on the social environment an animal experiences, for example, an individuals' own social phenotype (Webber and Vander Wal 2018) and spatiotemporal variation in population density (Morris 1987). Importantly, individual variation in social phenotypes can also be density-dependent (Bonenfant et al. 2009). My understanding of the adaptive value of density-dependent habitat selection and social phenotypes influences my ability to quantify individual-based traits and assess their influence on fitness components, including survival and reproductive success.

Density dependence of phenotypes influences population dynamics and demographic rates through feedback loops (Ezard et al. 2009; Pelletier et al. 2009) and is important in a behavioural context. Density fluctuates in natural populations, suggesting that individuals should display behavioural plasticity in response to fine-scale spatiotemporal changes in density

(Nicolaus et al. 2016). For gregarious species, group size (Bateman et al. 2012), social network centrality (O'Brien et al. 2018), and interaction duration (Brashares et al. 2010) are density-dependent, and the relationship between these traits and fitness is predicted to change as a function of population density (Webber and Vander Wal 2018). Individuals in social groups should therefore be equipped with adaptive behavioural tactics to cope with the potential for increased competition as a function of increasing density. The adaptive value of social behaviour and the potential for social plasticity in the context of density dependence is often ignored, yet the relationship between social behaviour and fitness has potential to influence, and be influenced by population-level density dependence (Webber and Vander Wal 2018; Vander Wal and Webber 2020).

Habitat selection is also density-dependent and can influence fitness. Density-dependent habitat selection occurs when individuals select habitat based on both habitat quality and the density of individuals present (Fretwell and Lucas 1969; Morris 1987). Habitat selection analyses are used to predict how populations, or individuals, select certain habitats compared to their availability (McLoughlin et al. 2010). Habitat selection phenotypes are predicted to vary among-individuals (Leclerc et al. 2016) and across densities (Webber and Vander Wal 2018). Two distinct bodies of literature provide predictions about how habitat and resource selection have evolved as functions of variation in population density. The Ideal Free Distribution (IFD) suggests that variation in density across different habitat patches leads to a fitness equilibrium where fitness in a habitat patch depends on density where, ideally, the available resources on a habitat patch can sustain a specific number of individuals (Bradbury et al. 2015). Density-dependent habitat selection is an extension of IFD theory and suggests that individuals at high population density are expected to be generalist consumers because competition for high quality

resources is high, while at low population density individuals are expected to be specialist consumers (Fortin et al. 2008). For example, red deer (*Cervus elaphus*) were grassland specialists at low densities but habitat generalists, as well as dietary generalists, at high densities (McLoughlin et al. 2006). By contrast, Optimal Foraging Theory suggests that competition at high population density is expected to increase individual specialization, i.e., the proportion of an individual's diet or resource use relative to the population's overall resource base (Svanbäck and Bolnick 2007; Tinker et al. 2008). For example, individual banded mongoose (*Mungos mungo*) increased their foraging specialization as group size and competition increased (Sheppard et al. 2018). Given these diverging predictions in habitat specialization it is also possible that individuals may display plasticity in their ability to specialize within their lifetime (Bolnick et al. 2003; Araújo et al. 2011).

Plasticity is variation in a given trait, including behavioural traits, as a function of variation in internal or external stimuli and has been extensively studied in evolutionary biology and developmental psychology (Stamps 2016; Stamps and Biro 2016). Within-individual behavioural plasticity, or flexibility, refers to the extent to which an individual's behaviour changes in different situations or in response to a given stimuli and this type of behavioural plasticity has been widely applied to the field of animal personality (Brommer 2013; Stamps 2016). Animal personality traits, defined as consistent individual differences in behaviour, are expected to persist through space and time and this variation may be adaptive (Smith and Blumstein 2008). The concept of individual differences in behaviour can be measured as three parameters: 1) behavioural plasticity: the ability of individuals to alter phenotypes as a function of the environment; 2) behavioural syndromes: correlated suites of behaviours across time or space; and 3) behavioural repeatability: the proportion of phenotypic variance attributable to

among-individual differences (Dingemanse et al. 2010). These parameters are examples of ways to operationalize the adaptive potential of behavioural phenotypes, such as social behaviour and habitat specialization, at individual or population-levels.

Here, I empirically quantified social association, habitat specialization, and fitness in six herds of a social ungulate (*Rangifer tarandus*) living across a population density gradient. First, I used proximity-based social network analysis to estimate social graph strength, which is the sum of weighted associations in a social network. Second, I estimated individual habitat specialization measured as the proportional similarity in resource use between individuals and the population. Third, I estimated fitness based on calf survival, an important fitness proxy in ungulates (Gaillard et al. 2000), including caribou (Bonar et al. 2018). I then used multi-variate behavioural reaction norms (BRNs) to estimate plasticity of social strength and habitat specialization across a population density gradient, covariance between social strength, habitat specialization, and fitness, and repeatability of all traits. I first tested predictions associated with Ideal Free Distribution and Optimal Foraging Theory (for details on each prediction see Table 6.1). First, independent of IFD and OFT, I predicted that individual values of social strength should increase with population density (P1). According to IFD and OFT, the relationship between habitat specialization and population density should differ, such that the IFD predicts individuals (or populations) should specialize as population density increases (P2a), while the OFT predicts individuals should generalize as population density increases (P2b). I did not expect the relationship between social strength and habitat specialization to vary for the IFD or OFT, so I predicted a positive relationship, such that more social individuals are habitat generalists (P3a and P3b). I expected that social strength and habitat specialization would be repeatable through space and time (P4a and P4b). The IFD predicts that at lower density, fitness

would be highest for more social individuals, while at higher density fitness would be highest for less social individuals (P5a), while the OFT does not have an intuitive directional prediction for the relationship between social strength and fitness across a density gradient (P5b). Finally, based on the IFD, I predicted that at lower density, fitness would be highest for individuals with a high degree of habitat specialization, while at higher density, fitness would be highest for individuals with a high degree of habitat generalization (P6a). By contrast, based on Optimal Foraging Theory, I predicted that at lower density, fitness would be highest for individuals with a high degree of habitat generalization, while at higher density, fitness would be highest for individuals with a high degree of habitat specialization (P6b). For more details on all predictions see Table 6.1.

6.3 Methods

6.3.1 Study Area and Subjects

We used GPS location data collected from six caribou herds in Newfoundland, Canada (Figure S6.1, for details see Appendix S6.1). Caribou population density in Newfoundland has fluctuated over time, such that herds peaked in size in the 1990s and declined in size in the 2000s (Figure S6.2; Bastille-Rousseau et al. 2013). Adult female caribou from all herds were immobilized and fitted with global positioning system (GPS) collars (Lotek Wireless Inc., Newmarket, ON, Canada, GPS4400M collars, 1,250 g, see Appendix S6.1 for details). Collars were deployed on 127 adult female caribou for one to three years, and collars were often re-deployed on the same individuals for up to seven years (3.2 ± 1.7) between 2007 and 2013. The number of collared individuals varied between herds, but the proportion of collared individuals in each herd was similar (Figure S6.3). Collars were programmed to collect location fixes every two hours, depending on the herd and year. Prior to analyses, I removed all erroneous and outlier GPS fixes

following Bjørneraas et al. (2010). Each relocation was assigned to a given habitat classification that was extracted from Landsat images with 30x30m pixels. Locations were categorized as one of eight habitat types: lichen barrens, wetland, rocky outcrops, water/ice, conifer scrub, mixed wood, or conifer forest (Lewis 2014). To assess potential for seasonal differences in social behaviour and habitat selection, I delineated GPS fixes into discrete 70-day periods to reflect winter (1 December–10 February) and calving (21 May–31 July), which I then used for all subsequent analyses. These seasons fall within previously identified seasonal periods that were identified based on caribou movement and life-history (Bastille-Rousseau et al. 2016). I chose to include winter and calving seasons because winter represents a resource limited season where adult female caribou form groups to optimize access to foraging resources (Peignier et al. 2019). Meanwhile, calving is a period when females aggregate on calving grounds or in large social groups and select habitat to reduce the risk of calf predation (Rayl et al. 2014; Bonar et al. 2020). All animal capture and handling procedures were consistent with the American Society of Mammologists guidelines (Sikes and Mammalogists 2016).

6.3.2 Population density estimates

Population size was estimated based on intermittent aerial surveys for each herd (see Figure S6.2; Mahoney et al. 1998; Lewis and Mahoney 2014). I estimated the area occupied (km^2) for each herd in each season and year by pooling GPS relocation data for all individuals and subsequently calculating the area of the 100% minimum convex polygon in the *adehabitatHR* package in R (Calenge 2006). I then estimated population density for each herd in each year and season by dividing the total number of animals estimated by the area (km^2) occupied by the herd.

To ensure convergence of subsequent models, population density was scaled and mean centered by herd to preserve variation in density between herds.

6.3.3 Social network analysis

I used the *spatsoc* package (Robitaille et al. 2019) to generate proximity-based social networks from GPS telemetry data. Traditional designation of caribou herds in Newfoundland assigns animals to specific herds, however, because of winter spatial overlap for some herds (Schaefer and Mahoney 2013), I constructed a single network for all collared animals in each year-by-season combination. I generated social networks based on proximity of GPS fixes for individual caribou. I assumed association between two individuals if simultaneous GPS fixes, i.e., recorded within 5 minutes of each other, were within 50 m of one another (Lesmerises et al. 2018). I applied the 'chain rule', where each discrete spatiotemporal GPS fix was buffered by 50 m and I considered individuals in the same group if 50 m buffers for two or more individuals were contiguous (Kasozi and Montgomery 2020). I weighted edges of social networks by the strength of association between dyads using the simple ratio index (SRI, for details on calculating the SRI see Appendix S6.2). Given recent discussion regarding the use of effect sizes and Bayesian inference to model social network analyses (Franks et al. 2020), I did not explicitly incorporate null models into my regression framework. Rather, I modelled social network strength in a Bayesian modelling framework (see below) and, following Farine (2017), I develop data-stream permutations to assess the potential for non-random social structure through space and time (see Figure S6.4 and Appendix S6.2).

6.3.4 Estimating habitat specialization

Based on landcover classification, my study area was separated into eight habitat types: conifer forest, conifer scrub, mixed-wood forest, deciduous forest, wetland, lichen barrens, rocky

barrens, and water/ice (Table S6.2). Using the number of spatial relocations for a given individual in each habitat type, I estimated the proportional specialization index (PS_i):

$$PS_i = 1 - 0.5 \sum_j |p_{ij} - q_j|$$

where p_{ij} describes the proportion of the jth habitat type for individual i, and q_j describes the proportion of the jth habitat type at the population level. Values of PS_i closer to one reflect individuals that select habitats in direct proportion to the population, i.e., habitat generalists, whereas values of PS_i closer to zero reflect individuals that are habitat specialists. I calculated the PS_i using the *RInSp* package in R (Zaccarelli et al. 2013). A value of PS_i was therefore calculated for each individual in each year-by-season combination and represented the degree to which that individual specialized on any given habitat type. To confirm habitat specialization was related to habitat selection (McLoughlin et al. 2010), I generated resource selection functions and compared the PS_i to habitat selection coefficients for the dominant habitat types (see Appendix S5.3, Figure S6.6).

6.3.5 Fitness estimates

We used calf mortality as a proxy for fitness for adult female caribou. Following DeMars et al. (2013) and Bonar et al. (2018) I retrospectively assessed calf mortality using a movement-based approach. Unlike other cervids, caribou only have a single calf per year. Parturition is related to reduced movement rate in caribou, and I used inter-fix step length from GPS collared caribou to infer parturition and calf mortality (for details on validation see Bonar et al. 2018 and application in Bonar et al. 2020). I applied a population-based method using a moving window approach to evaluate three-day average movement rates of adult females to estimate parturition status (DeMars et al. 2013), and an individual-based method that used maximum likelihood estimation and GPS inter-fix step length of adult females to estimate calf mortality up to four weeks in age.

Mothers that do not give birth have a consistent daily average movement through time, while mothers that give birth decrease step length immediately after birth and slowly return to daily average movement rates (see Fig 2. from Bonar et al. 2018). In cases where calf mortality occurs, the mother will return to daily average movement rate almost immediately after calf mortality (see Fig 2. from Bonar et al. 2018). The majority of calf mortality in my study was due to predation (Mumma et al. 2014; Mahoney et al. 2016). Based on results from these models, I estimated calf mortality for each individual caribou in each year, i.e., annual reproductive success, and used this value as a proxy for fitness (for details see Bonar et al. 2018).

6.4.6 Statistical analysis: behavioural reaction norms

Behavioural reaction norms (BRNs) estimate behavioural repeatability and plasticity. BRNs generate two key parameters: 1) the reaction norm slope, which corresponds to phenotypic plasticity; and 2) the reaction norm intercept, which corresponds to consistent individual differences in behaviour (Dingemanse et al. 2010). I employed a multivariate mixed model (R package 'MCMCglmm': Hadfield 2010) to quantify BRN components, i.e., repeatability and plasticity, for resource specialization, social strength, and fitness as a function of population density. I used multi-variate models to avoid the common problem of 'stats-on-stats', where best linear unbiased predictors (BLUPs) are extracted from one or more mixed models and used to represent an individual's phenotype in subsequent statistical models (for details see Hadfield et al. 2010; Houslay and Wilson 2017). Although BLUPs can be problematic if used in the context of 'stats-on-stats', my use of tri- and bi-variate models limits this issue by assessing the relationship between variables of interest and accounting for potential confounds in the same model (Houslay and Wilson 2017). To facilitate model convergence I scaled and centered social

strength and habitat specialization to a mean of zero.

We developed five multi-variate models. First, I parameterized a tri-variate global model that included calf survival as a proxy for fitness, social strength, and habitat specialization as co-response variables. In this model, I included year, season, scaled population density, and herd as fixed effects. Individual identity and mean and centre-scaled population density were included as random effects, where individual values of social strength and habitat specialization varied as a function of population density. Next, I parameterized four bi-variate models with calf survival and either social strength or habitat specialization as co-response variables for subsets of the data delineated based on either low or high density herds. Specifically, based on the distribution of scaled population density, I delineated the lowest quantile (i.e. lowest 25% of density values) as low density data, and the highest quantile (i.e. the highest 75% of density values) as high density data. I chose to separate data based on the lowest 25% and highest 75% values of population density to ensure there was no potential for error in assigning individuals to a density category or overlap of individuals in a given herd (e.g. if I used the upper and lower 50% as categories this would have been possible).

Based on my global model, I evaluated repeatability (r) of BRN intercepts for habitat specialization and social strength as the amount of between-individual variance (V_{ind}) attributable to the residual variance among groups (V_{res}) for each trait (Dingemanse and Dochtermann 2013):

$$r = \frac{V_{ind}}{(V_{ind} + V_{res})}$$

Within the global model, repeatability was estimated for social strength and habitat specialization during winter and calving seasons. I also examined correlations between habitat specialization, social strength, and fitness. Among-individual variance in resource specialization and social strength may differ based on whether population density is low or high, relative to the

overall average. I therefore varied residuals in my model by season because of differences in social tendencies and habitat selection for caribou across seasons (Bastille-Rousseau et al. 2016; Peignier et al. 2019). Thus, I calculated V_{res} and r for habitat specialization and social strength, for each season separately. I used uninformative priors (Wilson et al. 2010) and coded variance (s^2) as $s^2/2$ and degree of belief as four for fixed and random effects. I fit all models with Gaussian error structure for both response variables. I ran conservative Markov Chain Monte Carlo (MCMC) chains of 420,000 iterations, a thinning interval of 100, and a burn-in of 20,000. All analyses were conducted in R (version 1.1.383; R Core Team, 2017).

6.4 Results

We collected data for 127 individual caribou. In total, I calculated an average of 6 ± 3.5 (range: 1–14) measures of social strength, habitat specialization, and reproductive success per individual, for a total of 779 measures of these variables across all years and herds. Due to variation in length of time that collars were deployed on individuals seasonal networks were larger in winter (average: 66 ± 21 individuals, range = 35–90) than calving (average: 53 ± 26 individuals, range = 15–81). On average, social strength was higher in winter (mean = 0.012 ± 0.001) than calving (average: 0.005 ± 0.006). By contrast, habitat specialization indices were similar between winter (average: 0.72 ± 0.08) and calving (average: 0.72 ± 0.13). Habitat specialization was positively correlated with habitat selection coefficients generated from resource selection coefficients for all four habitat types, suggesting that as selection for a given habitat increased, the propensity to generalize also increased, and as selection for a given habitat weakened, the propensity to

specialize on a different habitat increased (Figure S6.6). My estimates of fitness indicated that calf survival was 61% (241/393 annual reproductive events).

We found support for my first hypothesis that social strength and habitat specialization would increase as a function of population density gradient (Prediction 1). Individuals varied their behavioural response to changes in population density, but in general, individuals became more social as population density increased (P1, Figure 6.1a, Figure S6.7). In addition, individuals also varied in their habitat selection patterns as population density changed, where the majority of individuals tended to become habitat specialists as density increased (P2a, Figure 6.1b, Figure S6.8). Although the direction of behavioural change was similar for most individuals, I observed variation in the magnitude of change, suggesting an individual by environmental interaction.

We found mixed support for predictions on phenotypic covariance (P3) and repeatability (P4). In my global model, I found strong phenotypic covariance between social strength and habitat specialization (0.52, 95% Credible Interval: 0.21, 0.79), suggesting that habitat generalists were more social and habitat specialists were less social (Figure 6.2). To determine the degree to which social strength and habitat specialization were repeatable across a population density gradient I estimated repeatability within and between seasons (P4). After taking herd, season, and year into account as fixed effects, I found that social strength was moderately repeatable during calving ($r = 0.25$, 95% CI: 0.15, 0.37), but not winter ($r = 0.03$, 95% CI: 0.015, 0.05). By contrast, habitat specialization was moderately repeatable in winter ($r = 0.20$, 95% CI: 0.11, 0.29), but not during calving ($r = 0.09$, 95% CI: 0.05, 0.14, Table 6.2).

When testing the relationship among social strength, habitat specialization, and fitness, I found support for Optimal Foraging Theory. In my global model, there was a positive

relationship between habitat specialization and social strength, where more social individuals were habitat generalists (P3a and P3b, 0.50, 95% CI: 0.17, 0.71, Table 6.3). In my global model, there was a weak negative relationship between habitat specialization and fitness (–0.29, 95% CI: –0.59, 0.03), but no relationship between social strength and fitness (–0.03, 95% CI: –0.36, 0.29, Table 6.3). When I modeled high and low density separately, there was no effect of social strength on fitness at either low or high density (P5a and P5b, Table 6.3). In support of Optimal Foraging Theory (P6b), and in contrast to the IFD (P6a), I found negative covariance between habitat specialization and fitness at high density (–0.62, 95% CI: –0.99, –0.01, Table 6.3), but no relationship between habitat specialization and fitness and low density (0.02, 95% CI: –0.81, 0.94, Table 6.3).

6.5 Discussion

Animals live by five fundamental principles that are distilled into resources, space use, competition, environmental variation, and reproduction (Morris 2003). I examined these principles by tested competing hypotheses about the relationships among habitat specialization, sociality, population density, and fitness. According to the Ideal Free Distribution, resource specialists maximize fitness at low population density (Fortin et al. 2008), while Optimal Foraging Theory posits that resource specialists maximize fitness at high population density (Tinker et al. 2008). The apparent tension between these two hypotheses could be mediated by consideration of variation in the social environment experienced by individuals (e.g. Sheppard et al. 2018). An increase in social connections across a population density gradient has potential to influence the propensity of individuals to successfully generalize or specialize. At high density, when individuals tend to be more social and competition for limited resources, individuals may specialize on different available resources to reduce competition (Newsome et al. 2015). Here, I

highlight that individual habitat specialization is density-dependent following predictions associated with optimal foraging, and the relationship between habitat specialization and fitness is moderated by individual social phenotypes.

Overall, I found support for my predictions associated with the Optimal Foraging Theory, where individuals tended to specialize on particular habitats at high population density (P6b). In banded mongooses (*Mungos mungo*), sea otters (*Enhydra lutris*), and stickleback (*Gasterosteus aculeatus*), individuals and populations tended to specialize at high population densities (Svanbäck and Bolnick 2007; Tinker et al. 2008; Sheppard et al. 2018). In addition to these empirical studies, my results support theory suggesting that population density is a mechanism driving variation in individual habitat specialisation (Bolnick et al. 2003; Araújo et al. 2011). The relationship between habitat specialization and fitness according to Optimal Foraging Theory is based on the assumption that individuals specialize on profitable resources and that this profitability results in increased fitness. Indeed, I found that higher fitness was achieved for habitat specialists at high density. Given that individuals consistently adjusted their habitat specialization behaviour as density changed, and that specialists had higher fitness at high density, fluctuating selection should favour variation in habitat specialization phenotypes. A potential mechanism explaining among-individual variation in habitat specialization is a mutual interest in avoiding competition in heterogeneous or patchy environments (Laskowski and Bell 2013). Given the adaptive value of habitat specialization, plasticity in habitat specialization from low to high density could be maintained as individuals alter their behaviour to adjust to environmental conditions.

In support of my prediction associated with the IFD, I found positive phenotypic covariance between social strength and habitat specialization, such that more social individuals

were habitat generalists (P3a, Table 6.3). Individual dietary and resource specialization are known to be strongly driven by competition (Bolnick et al. 2003). In a more competitive social environment, IFD theory predicts that individuals should generalize on resources or habitats to reduce competition. Social individuals may be constrained from specializing due to the competition associated with group living at high density. Moreover, theory of density dependence predicts that at high population density, reproductive success will be relatively low (Fowler 1981), and only a small proportion of individuals will successfully rear calves. Habitat generalists tend to be more social; a tactic which does not have an immediate effect on fitness. More social, habitat generalists, presumably obtain other benefits of group-living, such as increased vigilance and access to information about foraging resources. Although I was unable to test for life-history trade-offs, it is possible that more social individuals prioritize survival, as opposed to reproductive success, a trade-off that could have implications for population dynamics. Given observed plasticity in social behaviour and habitat specialization, these contrasting strategies present an apparent tension for individuals to simultaneously be habitat specialists *and* be highly connected in the social network.

Our integration of individual habitat specialization within a behavioural reaction norm framework highlights the ability for individuals to adjust their specialization phenotypes across a population density gradient. While plasticity in morphological traits is known to influence dietary specialization (Svanbäck and Eklöv 2006), behavioural plasticity of habitat specialization is less well understood. Despite relatively few empirical studies, plasticity in individual specialization reflects a natural extension from the expectations of individual niche specialization theory (Bolnick et al. 2003; Araújo et al. 2011), which posit contrary predictions to IFD. Individuals that experience a range of population densities within their lifetime should vary in

their habitat specialization-generalization phenotype (Dingemanse et al. 2010; Nicolaus et al. 2016). I found that individual caribou generally became more specialized as their population density increased, suggesting within-individual plasticity; a strategy that represents an individual's ability to adapt to changing environmental conditions. Since reproductive success is frequently depressed at high density (Charnov 1976; Morris 1989), my results suggest that only the most specialized individuals have greatest reproductive success, although it is possible that other ecological or behavioural factors could influence reproductive success. The ability for individuals to modulate their specialization behaviour across population densities therefore likely has adaptive consequences (Mathot et al. 2012). Moreover, habitat specialization was moderately repeatable, suggesting that the most specialized individuals at low population densities remain the most specialized at a higher density. Behavioural repeatability is important in an evolutionary context because repeatability represents the upper limit of heritability (Dochtermann et al. 2015), and ultimately, the adaptive value of habitat specialization suggests the potential for this trait to under-go natural selection. The tension between repeatability and plasticity therefore represents an interesting proximate – ultimate trade-off. Plasticity allows individuals to proximately adapt to current environmental conditions, while repeatability, and heritability, allows individuals and (if heritable) their descendants to display consistent responses to environmental conditions.

Animals use space, select habitat, and occupy social positions that maximize their fitness. By integrating theory of density dependence with competing hypotheses associated with the Ideal Free Distribution and Optimal Foraging Theories, I tease apart the effects of social and spatial behaviours as drivers of fitness. I present evidence supporting predictions associated with Optimal Foraging Theory that highlight the adaptive value of individual habitat specialization was greatest at high population density. Within the context of social eco-evolutionary dynamics

(Shizuka and Johnson 2020; Vander Wal and Webber 2020), my study addresses two of the criteria outlined as prerequisites for eco-evolutionary dynamics (Fussmann et al. 2007). First, previous work in this system has identified fluctuations in population density through time (Bastille-Rousseau et al. 2013) and although my study only included data from seven years, I observed slight differences in the distribution of habitat specialization as a function of population density (Figure 6.1). Second, I identified an effect of habitat specialization on fitness at high, but not low, density (Figure 6.3). Although estimating eco-evolutionary dynamics for behaviour remain elusive, I satisfy some of the baseline expectations of an eco-evolutionary correlation. Next steps include identifying a plausible mechanism link between an evolutionary, e.g. change in trait distribution, and ecological, e.g. lambda, process (Fussmann et al. 2007). It is clear that density dependence is a fundamental ecological process and I highlight the effects of population density on the relationship between behavioural phenotypes and fitness.

6.6 Acknowledgements

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Table 6.1: Summary of predictions.

General prediction	Prediction associated with Ideal Free Distribution	Prediction associated with Optimal Foraging Theory
P1: Density-dependent social strength. As density increases, individuals are expected to increase their social network strength.	P1a: No directional prediction.	P1b: No directional prediction.
P2: Density-dependent habitat specialization.	P2a: As density increases, individuals are expected to become habitat specialists (Fortin et al. 2008).	P2b: As density increases, individuals are expected to become habitat generalists (Pyke et al. 1977).
P3: Phenotypic covariance between social strength and habitat specialization (Webber and Vander Wal 2018).	P3a: More social individuals are expected to be habitat generalists.	P3b: More social individuals are expected to be habitat specialists.
P4: Repeatability of social strength and habitat specialization, such that behavioural traits are expected to be consistent through space and time (Bell et al. 2009).	P4a: Ideal Free Distribution is agnostic to the identity of individuals.	P4b: Within the framework of Optimal Foraging Theory and behavioural ecology theory, individual behaviours are expected to be consistent through space and time.
P5: Adaptive value of density-dependent social strength (Webber and Vander Wal 2018).	P5a: Low density: higher fitness for more social individuals High density: higher fitness for less social individuals	P5b: No directional predictions.
P6: Adaptive value of density-dependent habitat specialization.	P6a: Low density: higher fitness for habitat specialists High density: higher fitness for habitat generalists (McLoughlin et al. 2006; Fortin et al. 2008).	P6b: Low density: higher fitness for habitat generalists High density: higher fitness for habitat specialists Tinker *et al.* (2008).

Table 6.2: Summary of repeatability (r) estimates for caribou social strength and habitat specialization. Repeatability measures are a ratio between the proportion between-individual variance attributable to the residual variance (V_{res}) and therefore does not typically go below zero. High repeatability values are typically values of $r > 0.4$, moderate values of $r > 0.2$, but $r < 0.40$, and low values of repeatability are <0.20 (Bell et al. 2009). Values in brackets represent 95% credible intervals extracted from MCMC models.

Trait	Season	Median (±SD)	Repeatability	V_{res}
Social strength	Calving	0.005 ± 0.006	0.25 (0.15, 0.37)	1.54
	Winter	0.012 ± 0.015	0.028 (0.015, 0.05)	0.15
Habitat specialization	Calving	0.72 ± 0.13	0.09 (0.04, 0.14)	1.07
	Winter	0.72 ± 0.08	0.20 (0.11, 0.29)	0.44

Table 6.3: Phenotypic covariance among behavioural reaction norm intercepts for social strength, habitat specialization, and fitness in models with all data and separated into separate datasets where only data in the lowest 25% quantile, and highest 75% quantile, of population density were included. Numbers in brackets are 95% credible intervals and phenotypic covariance is considered significant if credible intervals do not overlap zero.

Trait combination	All data	Low density (25% quantile)	High density (75% quantile)
Social strength, habitat specialization	**0.50 (0.17, 0.78)**	–	–
Social strength, fitness	–0.03 (–0.36, 0.29)	–0.34 (–0.99, 0.86)	0.40 (–0.84, 0.99)
Habitat specialization, fitness	–0.29 (–0.59, 0.03)	0.02 (–0.81, 0.94)	**–0.62 (–0.99, –0.01)**

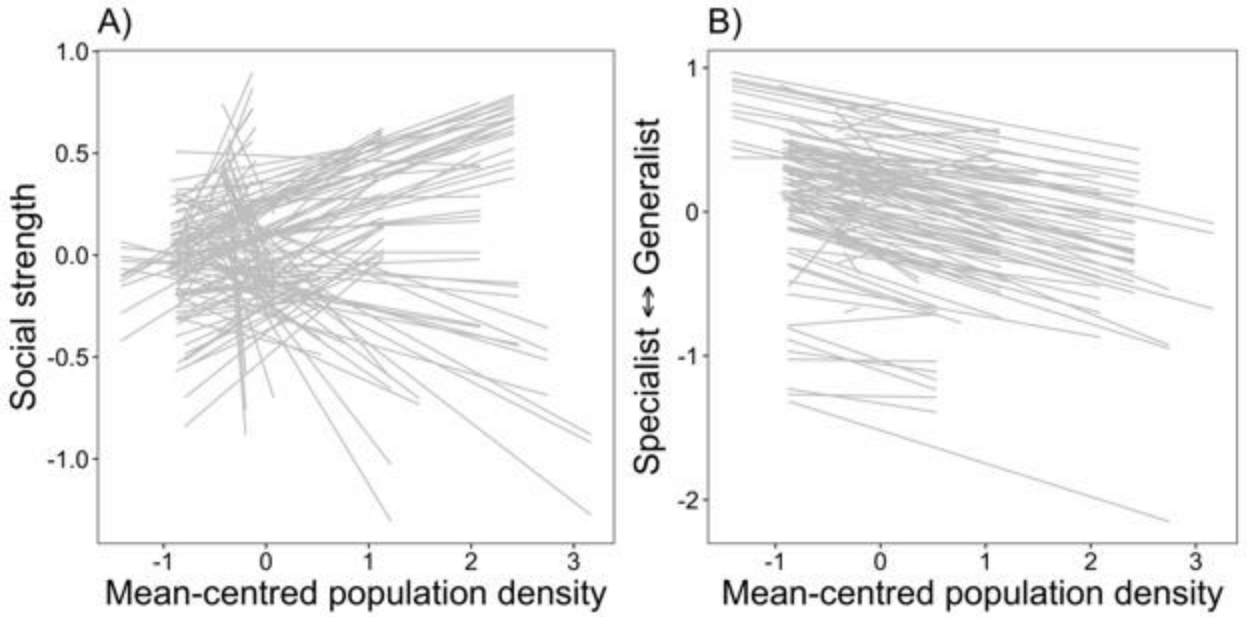

Figure 6.1: Behavioral reaction norms testing the relationship between population density and A) social network strength and B) habitat specialization for caribou (*Rangifer tarandus*; n = 127) in Newfoundland. Each line represents an individual behavioural response to changes in population density and crossing of lines represents individual differences in plasticity (i.e., an individual-environment interaction).

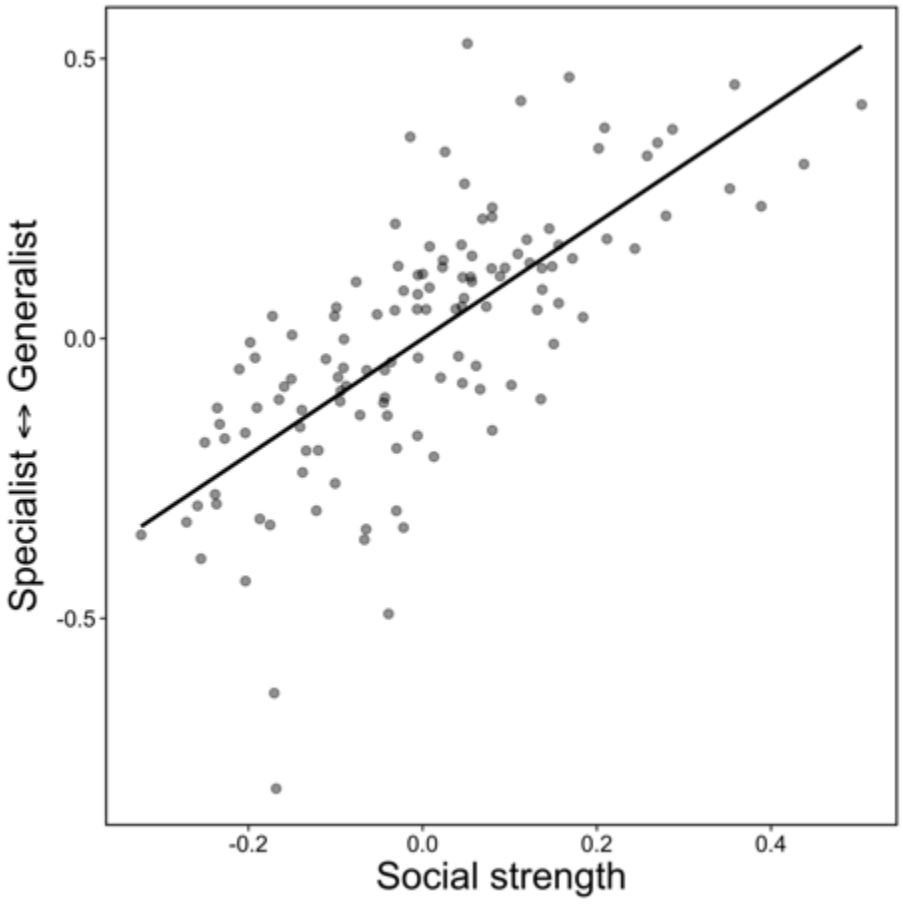

Figure 6.2: phenotypic covariance between social strength and habitat specialization in caribou (*Rangifer tarandus*, n = 127) in Newfoundland.

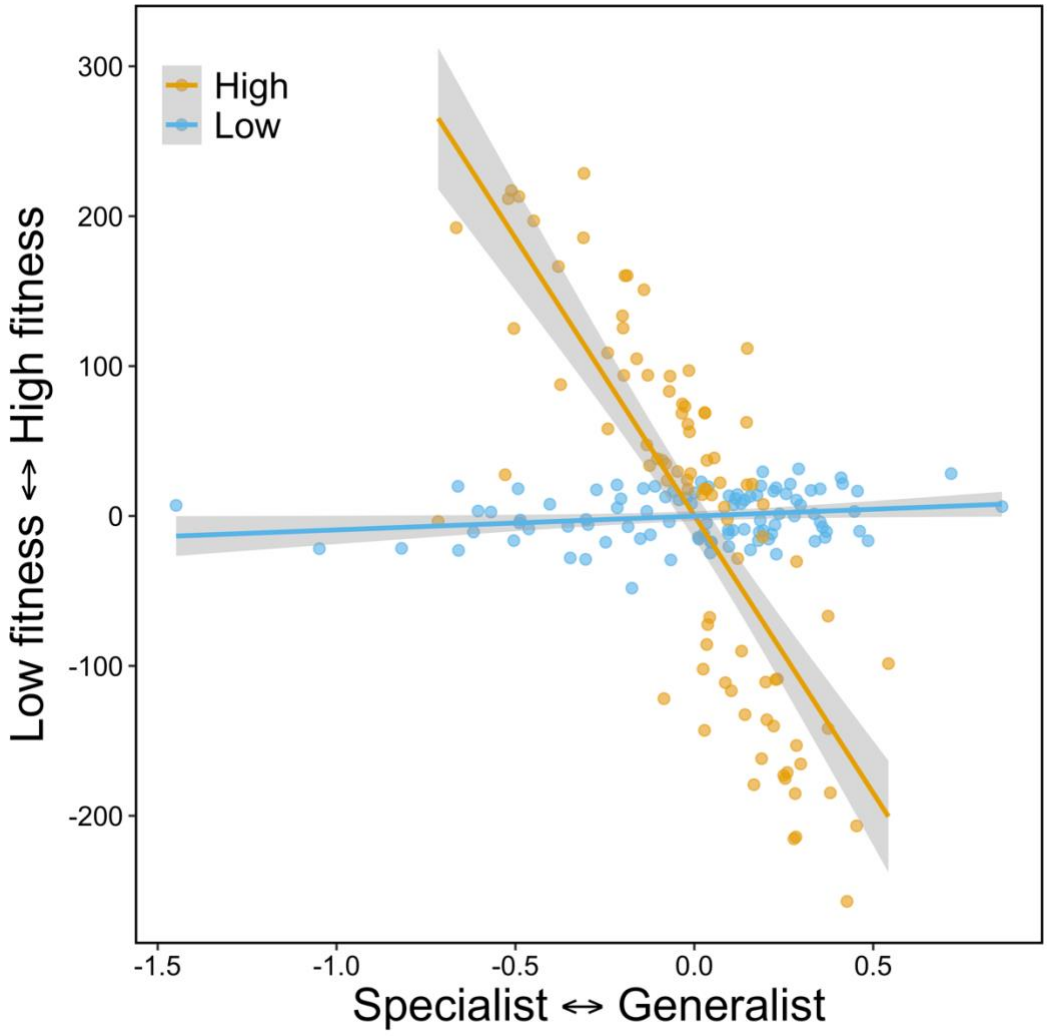

Figure 6.3: phenotypic covariance between reproductive success and habitat specialization at relatively high (orange points) and relatively low (blue points) population density for caribou (*Rangifer tarandus*, n = 127) in Newfoundland. At high density, more specialized individuals also tended to have an overall higher fitness value, whereas there was no effect of habitat specialization on fitness at low density. Note, both variables are extracted from best linear unbiased predictors (BLUPs) extracted from mixed models for visualization. Grey shaded areas represent 95% confidence intervals around best fit line.

6.7 References

Araújo MS, Bolnick DI, Layman CA. 2011. The ecological causes of individual specialisation. Ecol Lett. 14(9):948–958. doi:10.1111/j.1461-0248.2011.01662.x.

Bastille-Rousseau G, Rayl ND, Ellington EH, Schaefer JA, Peers MJL, Mumma MA, Mahoney SP, Murray DL. 2016. Temporal variation in habitat use, co-occurrence, and risk among generalist predators and a shared prey. Can J Zool. 94(3):191–198. doi:10.1139/cjz-2015-0127.

Bastille-Rousseau G, Schaefer JA, Mahoney SP, Murray DL. 2013. Population decline in semi-migratory caribou (Rangifer tarandus): intrinsic or extrinsic drivers? Can J Zool. 91(11):820–828. doi:doi:10.1139/cjz-2013-0154.

Bateman AW, Ozgul A, Coulson T, Clutton-Brock TH. 2012. Density dependence in group dynamics of a highly social mongoose, *Suricata suricatta*. J Anim Ecol. 81(3):628–639. doi:10.1111/j.1365-2656.2011.01934.x.

Bell AM, Hankison SJ, Laskowski KL. 2009. The repeatability of behaviour: a meta-analysis. Anim Behav. 77(4):771–783. doi:10.1016/j.anbehav.2008.12.022.

Bjørneraas K, Van Moorter B, Rolandsen CM, Herfindal I. 2010. Screening global positioning system location data for errors using animal movement characteristics. J Wildl Manage. 74(6):1361–1366. doi:10.2193/2009-405.

Bolnick DI, Svanbäck R, Fordyce JA, Yang LH, Davis JM, Hulsey CD, Forister ML. 2003. The ecology of individuals: Incidence and implications of individual specialization. Am Nat. 161(1):1–28. doi:10.1086/343878.

Bonar M, Ellington EH, Lewis KP, Vander Wal E. 2018. Implementing a novel movement-based approach to inferring parturition and neonate calf survival. PLoS One. 13:e0192204.

Bonar M, Lewis K, Webber QMR, Dobbin M, Laforge MP, Vander Wal E. 2020. Geometry of the ideal free distribution: individual behavioural variation and annual reproductive success in aggregations of a social ungulate. Ecol Lett. 23(9):1360–1369. doi:10.1111/ele.13563.

Bonenfant C, Gaillard JM, Coulson T, Festa-Bianchet M, Loison A, Garel M, Loe LE, Blanchard P, Pettorelli N, Owen-Smith N, et al. 2009. Empirical evidence of density-dependence in populations of large herbivores. Adv Ecol Res. 41(09):313–357. doi:10.1016/S0065-2504(09)00405-X.

Bradbury JW, Vehrencamp SL, Clifton KE. 2015. The ideal free antelope: foraging dispersions. Behav Ecol. 26(5):1303–1313. doi:10.1093/beheco/arv078.

Brashares JS, Werner JR, Sinclair ARE. 2010. Social “meltdown” in the demise of an island endemic: Allee effects and the Vancouver Island marmot. J Anim Ecol. 79:965–973. doi:10.1111/j.1365-2656.2010.01711.x.

Brommer JE. 2013. Phenotypic plasticity of labile traits in the wild. Curr Zool. 59(4):485–505. doi:10.1093/czoolo/59.4.485.

Calenge C. 2006. The package “adehabitat” for the R software: A tool for the analysis of space and habitat use by animals. Ecol Modell. 197:516–519. doi:10.1016/j.ecolmodel.2006.03.017.

Charnov EL. 1976. Optimal foraging theory: the marginal value theorem. Theor Popul Biol. 9:129–136. doi:10.1016/0040-5809(76)90040-X.

DeMars CA, Auger-Méthé M, Schlägel UE, Boutin S. 2013. Inferring parturition and neonate survival from movement patterns of female ungulates: A case study using woodland caribou. Ecol Evol. 3(12):4149–4160. doi:10.1002/ece3.785.

Dingemanse NJ, Dochtermann NA. 2013. Quantifying individual variation in behaviour: mixed-effect modelling approaches. J Anim Ecol. 82:39–54. doi:10.1111/1365-2656.12013.

Dingemanse NJ, Kazem AJN, Réale D, Wright J. 2010. Behavioural reaction norms: animal personality meets individual plasticity. Trends Ecol Evol. 25(2):81–89. doi:10.1016/j.tree.2009.07.013.

Dochtermann NA, Schwab T, Sih A. 2015. The contribution of additive genetic variation to personality variation: heritability of personality. Proc R Soc B. 282:20142201. doi:10.1098/rspb.2014.2201.

Ezard THG, Côté SD, Pelletier F. 2009. Eco-evolutionary dynamics: disentangling phenotypic, environmental and population fluctuations. Philos Trans R Soc Lond B Biol Sci. 364(1523):1491–1498. doi:10.1098/rstb.2009.0006.

Farine DR. 2017. A guide to null models for animal social network analysis. Methods Ecol Evol. 8(10):1309–1320. doi:10.1111/2041-210X.12772.

Fortin D, Morris DW, McLouglin PD. 2008. Habitat selection and the evolution of specialists in heterogeneous environments. Isr J Ecol Evol. 54(July):295–309. doi:10.1560/IJEE.54.3.

Fowler CW. 1981. Density dependence as related to life history strategy. Ecology. 62(3):602–610.

Franks DW, Weiss MN, Silk MJ, Perryman RJY, Croft DP. 2020. Calculating effect sizes in animal social network analysis. bioarXiv.:1–24.

Fretwell SD, Lucas HLJ. 1969. On territorial behaviour and other factors influencing habitat distribution in birds. Acta Biotheor. 19(1):16–36. doi:10.1007/BF01601953.

Fussmann GF, Loreau M, Abrams PA. 2007. Eco-evolutionary dynamics of communities and ecosystems. Funct Ecol. 21(3):465–477. doi:10.1111/j.1365-2435.2007.01275.x.

Gaillard J-M, Festa-bianchet M, Delorme D, Jorgenson J. 2000. Body mass and individual tness in female ungulates: bigger is not always better. Proc R Soc B.(November 1999):471–477.

Hadfield JD. 2010. MCMC methods for multi-respoinse generalized linear mixed models: The MCMCglmm R package. J Stat Softw. 33(2):1–22.

Hadfield JD, Wilson AJ, Garant D, Sheldon BC, Kruuk LEB. 2010. The misuse of BLUP in ecology and evolution. Am Nat. 175(1):116–125. doi:10.1086/648604.

Houslay TM, Wilson AJ. 2017. Avoiding the misuse of BLUP in behavioural ecology. Behav Ecol. 28:948–952. doi:10.1093/beheco/arx023.

Kasozi H, Montgomery RA. 2020. Variability in the estimation of ungulate group sizes complicates ecological inference. Ecol Evol.:1–9. doi:10.1002/ece3.6463.

Laskowski KL, Bell AM. 2013. Competition avoidance drives individual differences in response to a changing food resource in sticklebacks. Ecol Lett. 16(6):746–753. doi:10.1111/ele.12105.

Leclerc M, Vander Wal E, Zedrosser A, Swenson JE, Kindberg J, Pelletier F. 2016. Quantifying consistent individual differences in habitat selection. Oecologia. 180(3):697–705. doi:10.1007/s00442-015-3500-6.

Lesmerises F, Johnson CJ, St-Laurent M-H. 2018. Landscape knowledge is an important driver of the fission dynamics of an alpine ungulate. Anim Behav. 140:39–47. doi:10.1016/j.anbehav.2018.03.014.

Lewis KP. 2014. Sustainable Development and Strategic Science Branch Land Cover Classification.

Lewis KP, Mahoney SP. 2014. Caribou survival, fate, and cause of mortality in Newfoundland: a summary and analysis of the patterns and causes of caribou survival and mortality in Newfoundland during a period of rapid population decline (2003-2012). Tech Bull No 009, Sustain Dev Strateg Sci Gov Newfoundl Labrador, St John’s, NL.

Mahoney SP, Lewis KP, Weir JN, Morrison SF, Luther GJ, Schaefer JA, Pouliot D, Latifovic R. 2016. Woodland caribou calf mortality in Newfoundland: insights into the role of climate, predation and population density over three decades of study. Popul Ecol. 58(1):91–103. doi:10.1007/s10144-015-0525-y.

Mahoney SP, Virgl JA, Fong DW, MacCharles AM, McGrath M. 1998. Evaluation of a Mark-Resighting Technique for Woodland Caribou in Newfoundland. J Wildl Manage. 62(4):1227–1235.

Mathot KJ, Wright J, Kempenaers B, Dingemanse NJ. 2012. Adaptive strategies for managing uncertainty may explain personality-related differences in behavioural plasticity. Oikos. 121(7):1009–1020. doi:10.1111/j.1600-0706.2012.20339.x.

McLoughlin PD, Boyce MS, Coulson T, Clutton-Brock T. 2006. Lifetime reproductive success and density-dependent, multi-variable resource selection. Proc R Soc B. 273(1593):1449–1454. doi:10.1098/rspb.2006.3486.

McLoughlin PD, Morris DW, Fortin D, Vander Wal E, Contasti AL. 2010. Considering ecological dynamics in resource selection functions. J Anim Ecol. 79(1):4–12. doi:10.1111/j.1365-2656.2009.01613.x.

Morris DW. 1987. Tests of density-dependent habitat selection in a patchy environment. Ecol Monogr. 57(4):269–281.

Morris DW. 1989. Density-dependent habitat selection: testing the theory with fitness data. Evol Ecol. 3:80–94.

Morris DW. 2003. Toward an ecological synthesis: A case for habitat selection. Oecologia. 136(1):1–13. doi:10.1007/s00442-003-1241-4.

Mumma MA, Soulliere CE, Mahoney SP, Waits LP. 2014. Enhanced understanding of predator-prey relationships using molecular methods to identify predator species, individual and sex. Mol Ecol Resour. 14(1):100–108. doi:10.1111/1755-0998.12153.

Newsome SD, Tinker MT, Gill VA, Hoyt ZN, Doroff A, Nichol L, Bodkin JL. 2015. The interaction of intraspecific competition and habitat on individual diet specialization: a near range-wide examination of sea otters. Oecologia. 178(1):45–59. doi:10.1007/s00442-015-3223-8.

Nicolaus M, Tinbergen JM, Ubels R, Both C, Dingemanse NJ. 2016. Density fluctuations represent a key process maintaining personality variation in a wild passerine bird. Ecol Lett. 19:478–486. doi:10.1111/ele.12584.

O'Brien PP, Webber QMR, Vander Wal E. 2018. Consistent individual differences and population plasticity in network-derived sociality: An experimental manipulation of density in a gregarious ungulate. PLoS One. 13(3):e0193425.

Peignier M, Webber QMR, Koen EL, Laforge MP, Robitaille AL, Vander Wal E. 2019. Space use and social association in a gregarious ungulate: Testing the conspecific attraction and resource dispersion hypotheses. Ecol Evol. 9:5133–5145. doi:10.1002/ece3.5071.

Pelletier F, Garant D, Hendry AP. 2009. Eco-evolutionary dynamics. Philos Trans R Soc B. 364(1523):1483–1489. doi:10.1098/rstb.2009.0027.

Pyke GH, Pulliam HR, Charnov EL. 1977. Optimal foraging: a selective review of theory and tests. Q Rev Biol. 52(2):137–154.

R Core Team. 2019. R: A language and environment for statistical computing. :https://www.r-project.org/.

Rayl ND, Fuller TK, Organ JF, McDonald JE, Mahoney SP, Soulliere C, Gullage SE, Hodder T, Norman F, Porter T, et al. 2014. Mapping the distribution of a prey resource: neonate caribou in Newfoundland. J Mammal. 95(2):328–339. doi:10.1644/13-MAMM-A-133.1.

Robitaille AL, Webber QMR, Vander Wal E. 2019. Conducting social network analysis with animal telemetry data: applications and methods using spatsoc. Methods Ecol Evol. 10:1203–1211. doi:10.1111/2041-210X.13215.

Schaefer JA, Mahoney SP. 2013. Spatial dynamics of the rise and fall of caribou (*Rangifer tarandus*) in Newfoundland. Can J Zool. 91(11):767–774. doi:10.1139/cjz-2013-0132.

Sheppard CE, Inger R, Robbie A, Barker S, Emma IK. 2018. Intragroup competition predicts individual foraging specialisation in a group-living mammal. Ecol Lett. 21:665–673. doi:10.1111/ele.12933.

Shizuka D, Johnson AE. 2020. How demographic processes shape animal social networks. Behav Ecol. 31:1–11. doi:10.1093/beheco/arz025.

Sikes RS, Mammalogists AC and UC of the ASO. 2016. 2016 Guidelines of the American Society of Mammalogists for the use of wild mammals in research and education. J Mammal. 97(3):663–688. doi:10.1093/jmammal/gyw078.

Smith BR, Blumstein DT. 2008. Fitness consequences of personality: A meta-analysis. Behav Ecol. 19(2):448–455. doi:10.1093/beheco/arm144.

Stamps JA. 2016. Individual differences in behavioural plasticities. Biol Rev. 91:534–567. doi:10.1111/brv.12186.

Stamps JA, Biro PA. 2016. Personality and individual differences in plasticity. Curr Opin Behav Sci. 12(October 2017):18–23. doi:10.1016/j.cobeha.2016.08.008.

Svanbäck R, Bolnick DI. 2007. Intraspecific competition drives increased resource use diversity within a natural population. Proc R Soc B. 274:839–844. doi:10.1098/rspb.2006.0198.

Svanbäck R, Eklöv P. 2006. Genetic variation and phenotypic plasticity: causes of morphological and dietary variation in Eurasian perch. Evol Ecol Res.:37–49.

Tinker MT, Bentall G, Estes JA. 2008. Food limitation leads to behavioral diversification and dietary specialization in sea otters. Proc Natl Acad Sci U S A. 105(2):560–565. doi:10.1073/pnas.0709263105.

Vander Wal E, Webber QMR. 2020. Density dependence and eco-evolutionary dynamics of animal social networks: a comment on Shizuka and Johnson. Behav Ecol. 31:16–18. doi:10.1093/beheco/arz150.

Webber QMR, Vander Wal E. 2018. An evolutionary framework outlining the integration of

individual social and spatial ecology. J Anim Ecol. 87(1):113–127. doi:10.1111/1365-2656.12773.

Wilson AJ, Réale D, Clements MN, Morrissey MM, Postma E, Walling CA, Kruuk LEB, Nussey DH. 2010. An ecologist's guide to the animal model. J Anim Ecol. 79(1):13–26. doi:10.1111/j.1365-2656.2009.01639.x.

Zaccarelli N, Bolnick DI, Mancinelli G. 2013. RInSp: an R package for the analysis of individual specialization in resource use. Methods Ecol Evol. 4:1018–1023. doi:10.1111/2041-210X.12079.

CHAPTER 7:CONCLUSION

7.1 Summary

My thesis and the accompanying research narrative advances the understanding of social networks through incorporating theory, methods, and empirical integration of animal space use within social networks. I present evidence suggesting that social phenotypes vary through space and time and that both movement and spatial behaviours are inextricably linked to social behaviour with potential for one or more of these traits to influence fitness. Specifically, throughout my thesis I address five broad hypotheses that frame social behaviour, and the emergence of social networks, within a spatial context:

i) Individual social and spatial behavioural traits have a theoretical link to fitness through density dependence. A range of ecological and evolutionary processes are responsible for the relationship between social and spatial behaviour.

ii) Movement is the mechanistic link connecting social and spatial behaviour.

iii) Competition and the associated social interactions emerge from spatial variation in the availability of food.

iv) Groups are formed based on density dependence but spatial and temporal variation in resources also influences group size.

v) Social network traits and habitat specialization are density-dependent and the correlation between these behaviours affects fitness across a density gradient.

My thesis narrative can be summarized in three distinct areas which I discuss in this conclusion chapter. First, I address the role of social networks in a spatial context with special emphasis on the importance of integrating movement ecology, incorporating spatial phenotypes with models of social network analysis, and the potential for spatial features of the landscape to act as bottom-

up drivers of social network structure and organization. Second, I discuss the integration of classic ecological theory with our contemporary understanding of among-individual variation in behaviour. Specifically, I discuss the potential role of individuals within the Ideal Free Distribution and Optimal Foraging Theories as well as optimal group size theory. Finally, I conclude by framing my results within a broad conservation behaviour framework. I address the potential for Allee effects in caribou as well as the effect of habitat fragmentation and human-induced environmental change as drivers of change in the social environment that caribou experience. My thesis is a comprehensive document which bridges numerous theoretical frameworks (Figure 7.1) with an underlying motivation to better understand the behavioural ecology of a federally listed species at risk.

7.2 Social Networks in a Spatial Context

Animal social networks do not occur in a vacuum. Yet, despite this fact, social networks constructed from animal interactions or associations are often considered independent from the space those animals occupy. Animal space use can be considered as two central components: geographic and environmental space (Van Moorter et al. 2016). Geographic space concerns the position, size, and location of animal home ranges and the physical attributes of those ranges (Moorcroft 2012), while environmental space concerns the quality and quantity of resources and habitats (Manly et al. 2002). Taken together, geographic and environmental space influence the formation and maintenance of social networks (Spiegel et al. 2016; Pinter-Wollman et al. 2017). Animals may be more likely to form groups in certain habitats (Barja and Rosellini 2008), at certain times of year (Peignier et al. 2019), or based on physical constraints of the environment (Pinter-Wollman 2015), all of which are related to characteristics of geographic or environmental space (Chapter 5). The emerging idea that animal space use influences social networks has

become an important topic in the field of animal socioecology (Webber and Vander Wal 2018), but a unified theoretical framework linking animal behavioural, spatial, and population ecology remains elusive. We argue that social networks, and by extension the social environment, are inherently driven by underlying patterns of geographic and environmental space.

7.2.1. Integrating principles of movement ecology

The movement ecology framework can be described as an integration of the causes and consequences of movement for the ecology and evolution of individuals or populations (Nathan et al. 2008). Patterns of animal movement act as the mechanism driving behavioural decisions of animals. It is clear the causes and consequences of movement vary for individuals across a range of ecological contexts (Shaw 2020) and it is becoming increasingly clear that animal movement undoubtedly affects social networks (Strandburg-Peshkin et al. 2015; Jacoby and Freeman 2016). Movement has been cited as the 'glue' that connects geographic and environmental space (Chapter 4; Van Moorter et al. 2016). It has become increasingly clear that movement is also the 'glue' that connects the social environment to the underlying geographic and environmental space, hereafter the physical environment (Chapter 3). As animals navigate the physical environment to search for resources or to avoid predators, they often do so based on collective movements (Jolles et al. 2019). Collective movement can reduce group-level predation via detection-dilution trade-offs, and can also improve the efficiency of information transfer about the quality or location of resources (Jolles et al. 2019). Individuals in groups that move collectively experience the same physical environment, but individuals should theoretically position themselves within the group to minimize predation and maximize access to resources (Dostie et al. 2016). The spatial arrangement of individuals within moving groups is therefore highly dynamic and expected to alter social network structure on a near continuous basis.

Further complicating collective movement is the potential for fission-fusion, where groups merge and split through space and time. The adaptive value of fission-fusion lies in the ability for groups to balance the costs and benefits of social grouping, i.e. fission to avoid competition during foraging and fusion to improve information transfer and reduce risk of predation (Sueur et al. 2011). Variation in the physical environment therefore motivates individuals to space away from each other during foraging (Jacobs 2010). Fission-fusion in the form of movement to, from, or within habitat patches could also contribute to the formation of social networks (Spiegel et al. 2016). Context-dependent social networks emerge when animals interact or associate in different habitats or while engaging in different types of behaviours. For example, giraffes (*Giraffa camelopardalis*) associate more strongly during foraging than during movement between foraging patches (Muller et al. 2018). Fission-fusion dynamics could explain context-dependent sociality, where the emergence of social networks varies as animal groups fission and fusion through space and time. I argue that incorporating movement ecology within a social network framework is a logical extension of socioecological theory. In particular, when social networks are related to the physical environment, I suggest the integration of movement within social networks provides novel insight about the formation and maintenance of the social environment (He et al. 2019).

7.2.2 Spatial behaviours as a phenotype

While aspects of the physical environment undoubtedly influence social networks, individual-level space-use phenotypes should also be correlated to social phenotypes. Recent empirical studies have demonstrated that spatial phenotypes, including habitat selection (Leclerc et al. 2016), habitat specialization (Chapter 6), and area restricted search (Webber et al. 2020), display consistent within- and between-individual variation. Several mechanisms exist to explain

consistency in spatial phenotypes, including extrinsic and intrinsic mechanisms. Functional response in habitat selection (Mysterud and Ims 1998) is the premise that patterns of habitat selection should vary among individuals based on the relative availability of resources or habitats on the landscape (Holbrook et al. 2019). Individuals may only experience a subset of the resources available to the population, which could result in variation in patterns of selection and specialization (i.e., spatial phenotypes) (Duparc et al. 2019). Alternatively, spatial phenotypes could be driven by intrinsic physiological, innate, or genetic mechanisms. Individuals differ in their physiological requirements, which may lead to segregation of physiological phenotypes by habitat (Jolles et al. 2019). Variation in habitat selection may also be related to natal habitat preference (Stamps et al. 2009) or be a learned behaviour (Nielsen et al. 2013). Regardless of the mechanism, it is becoming increasingly apparent that individuals vary in their spatial phenotypes, and given the link between the social and physical environments (Figure 7.1), it is logical to assume that spatial phenotypes are correlated to social network phenotypes (Chapter 2; Webber and Vander Wal 2018). While correlation does not always mean causation, I argue that an effect of social phenotypes on fitness may in fact occur as a result of correlations with spatial phenotypes (Figure 7.1). Indeed, in Chapter 6, I show that spatial, and not social, phenotypes influence annual reproductive success.

While there is clear potential for spatial phenotypes to be important drivers of fitness relative to social phenotypes, some spatial phenotypes could influence the physical environment an individual, or group, experiences. Not only do spatial phenotypes have the ability to influence social phenotypes, they can also influence spatial phenotypes of other individuals. As a result, social and spatial phenotypes may emerge from the properties of animal assortment on the landscape. From a movement ecology perspective, it is possible individuals that are more likely

to lead groups may have a disproportionate effect on the spatial phenotypes of other group members (Jolles et al. 2019). From a habitat selection perspective, individuals may aggregate at high quality resources (Chamaillé-Jammes et al. 2008), a scenario where a spatial phenotype influences a social phenotype. In Chapter 3, I highlight the role of habitat selection for foraging resources as a potential driver of collective movement, but solitary foraging. Similarly, in Chapter 4, resource quality influenced social interactions within and between sexes. These examples highlight the integrated nature of social and spatial phenotypes. I suggest the integration of habitat selection (Morris 2003; Morris 2011) and movement ecology (Nathan et al. 2008) theories within social networks represents an advancement in our understanding of the causes and consequences of an animal social behaviour.

7.2.3 Bottom-up social networks

Hinde (1976) proposed a bottom-up approach for studying animal societies using three levels: interactions, relationships, and structure. This hierarchical approach relies on understanding one level before understanding the next. Patterns of interactions between individuals are used to describe relationships, and social structure is inferred based on the patterns of relationships (Hinde 1976). Many studies of social behaviour are inherently bottom-up from the perspective that social interactions influence social relationships, which in turn influence social structure. For example, Farine and colleagues (2012) outline the use of a bottom-up approach for understanding multi-species flocking in birds. Bottom-up social behaviour can also be state-based (e.g., hunger or other internal motivations) or based on the social decisions of individual animals (Cantor et al. 2020). While the expectation that social processes are bottom-up based on a hierarchical approach to social behaviour (Hinde 1976), this argument is an inherently social perspective. When expanding to consider other aspects of an animal's life, I argue that spatial

features of the landscape are equally, if not more, important drivers of bottom-up social structure.

Social network analysis enables a bottom-up examination of the social environment (Farine et al. 2012) and consideration of the underlying resources, physical environment, or spatial constraints that can result in an emergent social environment (Chapters 3, 4, 5, and 6). Despite the fact that many animals display strong social preference for one another, either as a result of natal philopatry, kin-based grouping, or other factors, it is clear that animals display consistent and long-term social relationships (Chapter 3). However, although social relationships are developed based on patterns of interactions among individuals, patterns of interactions can be affected by environmental variation (Chapter 4). Discarding information about underlying spatial heterogeneity could bias our interpretation of social networks and present challenges in the way we think about the ecology and evolution of social organization through the lens of network analysis. Three important considerations are: 1) is the animal foraging, resting, or moving? In many species, these behaviours take place in different environments or habitats and environment-specific behaviour can translate to social processes (Chapter 3; Muller et al. 2018). 2) Are interactions or associations happening as a result of competition for food? Many types of social interaction are not necessarily tied to any underlying spatial variation in the abundance or quality of food (e.g. allo-grooming or mating), but competition for food inherently assumes that individuals are either foraging or searching for forage (Chapter 4). 3) Is a spatial phenotype driving the social network trait? If possible, understanding how animals select for, or specialize on, resources could inform the formation and maintenance of social networks (Chapter 6). My thesis broadly addresses these three considerations and weaves together a narrative that highlights the importance of space as a bottom-up driver of social networks.

7.3 Extending Ecological Theory to Individuals within Social Networks

7.3.1 Integrating competition, ideal free distribution, and optimal foraging theory

Classic habitat selection theory is based on the Ideal Free Distribution (IFD), which posits that animals select habitat to maximize fitness (Fretwell and Lucas 1969). Similarly, Optimal Foraging Theory (OFT) presents an equivalent series of predictions within the framework of niche specialization. IFD predicts that habitat selection is density-dependent and variation in density between habitat patches leads to a fitness equilibrium (Bradbury et al. 2015). By contrast, OFT predicts that individuals should vary in their dietary breadth, and that this variation can be density-dependent (Araújo et al. 2011). The available resources within a habitat patch sustain a certain number of individuals and in a finite world, fitness in a habitat is predicted to decline after a critical threshold as a function of density (Morris 1987; Morris 2011). Importantly, the amount of food an animal obtains in a habitat patch depends on the density, or quality, of the food and the potential for interference competition from other animals present. Consumers are therefore predicted to aggregate in high quality patches, but space apart to reduce competition (Sutherland 1983). Despite the fact the IFD predicts individuals should assort in space to equalize fitness, these predictions omit the identity of individuals. Similarly, many of the predictions associated with OFT have historically been considered at the species level, although the concept of between-individual variation in niche breadth has been around for several decades (Bolnick et al. 2002; Araújo et al. 2011).

Interference competition is a behavioural interaction that occurs between individuals that reduces an individual's access to shared resources (Cresswell 1998). Examples of interference competition include kleptoparasitism or disturbance in search effort. Models predict that animals should assort such that competition at higher quality patches is equivalent to lower quality

patches (Sutherland 1983; Moody and Houston 1996). Under the assumption that competition for resources is an individually quantifiable phenotype (Parker and Sutherland 1986), theory on how individuals compete with one another could help further extend the concepts of IFD and OFT to individuals.

Social network analysis is an important tool that could help bring our understanding of the broad ecological theories from the population level to individuals (Chapter 6). For example, network traits could be used to parameterize models of IFD and OFT such that within patches individuals may adaptively vary in their social behaviour. Similarly, network traits could be used to estimate variation in competitive abilities, where superior competitors may be more likely to secure higher quality patches.

My integration of interference competition (Chapter 4) with IFD and OFT (Chapter 6) was indirect, but the broad narrative of my thesis suggests these ideas are linked and could be merged. Future studies should consider experimental manipulation of density and the phenotypic composition of social groups to determine whether individuals with certain social network traits are more likely to settle on patches in an ideal free manner.

7.3.2 Optimal group size theory

The optimal group size hypothesis posits that intermediate-sized groups represent a balance between competition and risk of predation. On one hand, the benefit of aggregation in larger groups is lower per capita risk of predation, while the costs to larger groups are increased competition. Groups range in size from one to a given maximum size, where fitness is maximized at an intermediate group size (Williams et al. 2003). Animals are therefore predicted to balance the costs and benefits of grouping and form groups of optimal size where fitness is maximized (Higashi and Yamamura 1993). In the context of the costs and benefits of sociality,

optimal group size balances predator vigilance and competition for foraging resources such that fitness is highest. However, criticisms of the optimal group size hypothesis are that groups increase in size beyond the optimal size (Williams et al. 2003). For species with fission-fusion dynamics there is likely no one optimal group size (Chapter 5; Gerard et al. 2002), and the size of a group at any given time depends on context, and will vary in size based on a species behaviour, ecology, and life-history (Webber and Vander Wal 2018). Groups are clearly important units within a network, while little discussion exists about how optimal group size theory extends to animal social networks.

In Chapter 5, I invoke optimal group size theory to help explain the potential for context-dependent grouping in caribou, but in theory, the same could be applied to social networks. So-called 'optimal social networks' could be an extension of optimal group size theory, where there is a given size, or density of edges, where fitness is maximized. Social networks are highly dynamic, so variation in network structure through space and time could be an important driver of network-level and individual-level effects on fitness. Most research on the link between social networks and fitness suggests that more social individuals tend to have higher fitness (Snyder-Mackler et al. 2020), but increasingly there are studies highlighting the existence of a negative relationship between sociality and fitness (e.g. Menz et al. 2020). Given the range of social effects on fitness, it is possible for an optimal network to exist where there is some optimal, or potentially intermediate size, density of edges, where fitness is maximized. Future work should address the potential for network-level attributes to fit within the existing optimal group size framework.

7.4 Conservation Implications

Caribou are in decline throughout their range (Vors and Boyce 2009), including in Newfoundland (Bastille-Rousseau et al. 2013). My research highlights some of the behavioural consequences associated with changes in population density as well as the relationship between social and spatial behaviour and fitness. The extension of my work to caribou conservation therefore lies in the relationship between behaviour and population density.

7.4.1 Human induced rapid environmental change and caribou

Caribou are clearly sensitive to environmental change. Particularly in areas where human modified landscapes are common, caribou alter their movement, habitat selection, and social behaviour as a result of encroaching human development (Weir et al. 2007; Dickie et al. 2020). For caribou, the conceptual link between social and spatial behaviour (Webber and Vander Wal 2018) logically extends to habitat fragmentation and human-induced rapid environmental change (HIREC). Recent empirical work from western Canada shows that caribou can respond to naturally occurring environmental change, but not anthropogenic disturbance or HIREC (Stewart et al. 2020). Thus, within an evolutionary ecology framework, the behavioural trait distribution observed in a population can cope with natural change. HIREC can expedite the mismatch between existing trait distributions that has evolved to cope with natural disturbances and the novel environments that have been altered due to HIREC and other anthropogenic disturbance.

To thrive, caribou typically require large tracts of mature coniferous forests and peatlands with relatively low density of competitors and predators (James et al. 2004; Bowman et al. 2010). Anthropogenic disturbance, habitat fragmentation, and HIREC could potentially disrupt the ability for herds to remain cohesive and use the same sites through time (Schaefer and Mahoney 2013; Prichard et al. 2020). Fragmentation that disrupts caribou spatial phenotypes,

such as site fidelity, habitat selection, and resource specialization, could be a bottom-up driver of changes to social network structure (Lafontaine et al. 2019; Prima et al. 2019). In these cases, knowledge of the landscape may disrupt the ability for individual caribou to use, or return to, the same spatial locations (Lafontaine et al. 2017). The social consequences associated with habitat fragmentation include disruption to social hierarchies and fragmentation of social groups. My thesis clearly highlights that caribou have preferred social relationships (Chapter 3) and if these individuals are separated as a result of habitat fragmentation, it is possible that other social processes, including information transfer about resources, could be affected (Peignier et al. 2019).

Currently, the link between anthropogenic disturbance and social structure in caribou is theoretical. I propose a series of potentially applied questions based on my results (Table 7.1). Although my results are focused within a broad theoretical and behavioural context, I strongly believe in the importance of applying my research to caribou conservation. I have therefore presented discussion of my results within the conservation behaviour framework and I highlight numerous areas for future applied research within the field of caribou socioecology (Table 7.1).

7.4.2 Allee effects in caribou

Understanding how births and deaths vary as a function of population density is a clear mandate of evolutionary and population ecology (Pelletier et al. 2007). Most empirical research suggests negative density dependence, where birth rates are low at high density (Fowler 1981), although inverse density dependence, or Allee effects, are also possible (Stephens et al. 1999). Allee effects are a density-dependent phenomenon that occurs when average individual fitness is positively correlated with population size or density in small populations (Berec et al. 2007). Allee effects are typically manifested as component (i.e. individual fitness) or demographic (i.e.

total fitness) effects (Stephens et al. 1999). The interplay between component and demographic Allee effects is such that one component Allee effect (e.g., individual survival) could be cancelled out by negative density dependence in a different component (e.g., individual reproduction) and result in no demographic Allee effect (Angulo et al. 2013). The presence of a demographic Allee effect therefore implies the presence of at least one component Allee effect (Stephens et al. 1999), while in nature, component Allee effects are relatively common and demographic Allee effects are relatively rare (Kramer et al. 2009; Gregory et al. 2010). Moreover, presence of a demographic Allee effect does not provide information about its mechanism, a process which requires detailed examination of the underlying component effect.

There is some evidence for Allee effects in caribou (Wittmer et al. 2005; McLellan et al. 2010). Specifically, the primary mechanism cited for Allee effects in caribou is predator-mediated (McLellan et al. 2010). The link between Allee effects and predation exists through social behaviour (Angulo et al. 2013; Angulo et al. 2017). While Allee effects have been demonstrated in asocial species, social species are thought to be particularly vulnerable to Allee effects (Angulo et al. 2013; Angulo et al. 2017). For instance, social aggregation, cooperative defense, and vigilance are predicted to reduce the per capita risk of predation (Lima and Dill 1990; Fryxell et al. 2007). Social species could therefore be prone to predator-mediated Allee effects because small groups or populations may be less able to detect, or defend against, predators (Wittmer et al. 2005; McLellan et al. 2010; Bourbeau-Lemieux et al. 2011). For example, small mountain caribou populations in British Columbia display inverse density dependence as a consequence of high mortality rates by predation (Wittmer et al. 2005). In this system, caribou exist at low density on the landscape compared to other ungulates and are therefore a secondary, or even incidental, prey for most predators (Wittmer et al. 2005). Thus,

while grouping is predicted to reduce predation rates (Hamilton 1971; Lima 1995), the likely mechanism driving Allee effects in caribou is declining group size as a function of declining population size (McLellan et al. 2010). Due to their small size, the per capita risk of predation is relatively high for caribou when they are encountered by predators. Thus, in theory, as groups decline in size with population density, the risk of predation increases and Allee effects could ultimately result in extirpation.

Interestingly, I found a positive relationship between group size and population density in herds varying in size from a few hundred to tens of thousands of individuals (Chapter 5). While Allee effects are typically only possible for small populations, it is possible that some smaller herds in Newfoundland experienced Allee effects during their declines. While predators appear to mediate Allee effects for mountain caribou, this mechanism is less likely for caribou in Newfoundland. Specifically, while coyotes and black bears are the primary driver of caribou calf mortality (Mumma et al. 2014; Rayl et al. 2015), risk of predation by these predators is much lower for adults (Lewis and Mahoney 2014). For caribou populations that experience relatively low predation, a possible mechanism explaining Allee effects is conspecific attraction and information transfer among conspecifics about novel, or changing, resources (Peignier et al. 2019). Given my findings that caribou move collectively between foraging patches, but forage solitarily (Chapter 3), it is likely that caribou use information transfer about the location and quality of resources. Moreover, it is clear that in winter, when the distribution and availability of resources is uncertain, caribou form larger and more cohesive groups, presumably to exploit information from conspecifics (Chapter 3; Chapter 5; Peignier et al. 2019). However, despite this possibility, information transfer as a mechanism driving Allee effects remains a relatively under-

explored aspect of density-dependence and Allee effects in social species (but see Schmidt *et al.* 2015).

For species with fission-fusion dynamics, like caribou, group size and composition can change across daily or seasonal time-scales (Chapter 5). Specifically, fission-fusion groups merge and split forming many sub-groups that, taken together, reflect a single large group. Social groups are highly dynamic for fission-fusion species and variation in the relationship between social grouping and fitness could reflect either component (individual) or demographic (group) Allee effects. Information transfer in fission-fusion societies is therefore an important mechanism that incorporates aspects of predator avoidance, foraging, and habitat selection. Although I did not measure Allee effects, my thesis (specifically Chapters 3 and 5) has direct implications for our understanding of Allee effects in caribou.

7.5 Concluding remarks

My thesis, and thesis-adjacent, research presents a broad over-arching story about how social processes are related to variation in the physical environment (Chapter 2). I examined how social association and habitat selection are linked through movement and found that caribou show distinct patterns of context-dependent social association between foraging and moving (Chapter 3). Caribou compete for resources and in Chapter 4, I tested the interference competition hypothesis. I found limited support for interference competition in female caribou, but I did find support for the male harassment hypothesis, suggesting that as groups increase in size, females face greater levels of harassment from males (Chapter 4). Patterns of ungulate group size are expected to vary spatially and temporally and in Chapter 5, I examined how group size changes as a function of population density, habitat type, and season. In contrast to past studies, I found evidence for a negative relationship between population density and group size as well as distinct

larger groups in winter compared to summer and calving (Chapter 5). Finally, I examined the effect of social and spatial phenotypes on fitness across a population density gradient within the context of the Ideal Free Distribution and Optimal Foraging Theory. I found broad support for Optimal Foraging Theory. Specifically, more social individuals tended to be habitat generalists, while at high population density, habitat specialists tended to have higher fitness, suggesting a tension between social and spatial phenotypes and an effect on fitness.

The social and physical environments are inextricably linked. I propose that movement ecology is a key, and missing, part of this link. The recent rise in popularity of social networks (Webber and Vander Wal 2019) has resulted in a wide range of uses and applications of social networks, however, the integration of animal movement and space use remains largely absent. My view is that social networks, and the corresponding social environment, are formed by bottom-up spatial processes where networks emerge from variation in how animal groups move through the physical environment. Ample empirical evidence exists supporting this claim (Pinter-Wollman et al. 2017; Spiegel et al. 2018), and my thesis presents the notion linking movement ecology within this narrative such that: physical environment $\rightarrow$ movement $\rightarrow$ social networks and habitat selection $\rightarrow$ fitness (Figure 7.1).

Table 7.1: Summary of potential future applied conservation behaviour studies based on results from my thesis.

Chapter	Result	Future study or hypothesis
3	Social association is context dependent; caribou move together, but forage apart (Figure 3.2)	Do changes in the composition and abundance of caribou food resources influence the existing social structure? In a future scenario where forage is lower in quality and quantity, do caribou space out (fission) far enough such that social groups are less likely to merge (fusion)?
4	Male harassment increases as a function of group size (Figure 4.4)	We assume that females suffer a somatic cost when they are harassed by males. How does this somatic cost differ for females depending on variation in habitat fragmentation and the quality and quantity of food available to them?
5	Groups decrease in size as density increases (Figure 5.2).	As density increases and groups become smaller what is the role of habitat fragmentation and human-induced rapid environmental change?
6	Habitat generalists are more social than habitat specialists (Figure 6.2).	On landscapes fragmented due to human activities, habitat generalists should perform better than habitat specialists. However, social groups may become separated in fragmented landscapes, thus disrupting the relationship between an individual's ability to generalize and remain socially connected.

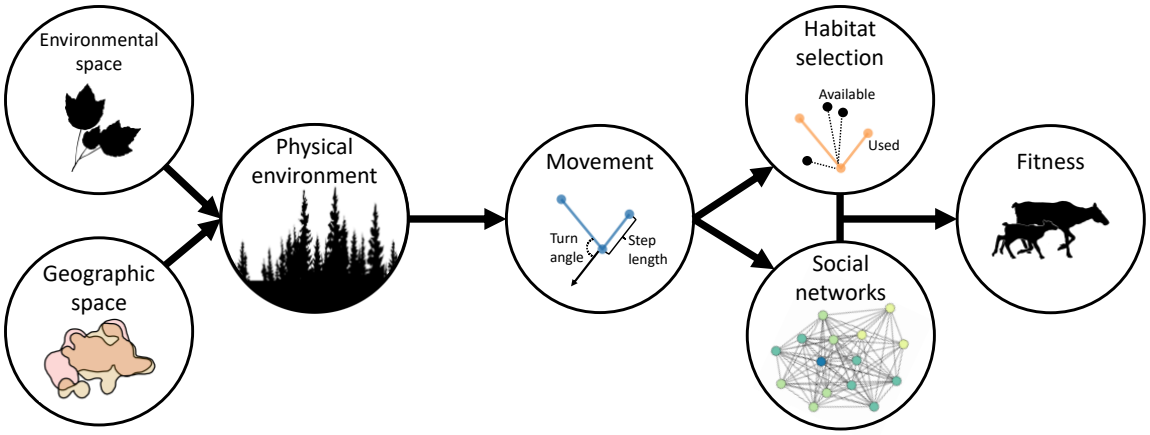

Figure 7.1: Illustration of how the physical environment (comprised of environmental and geographic space) influence movement, which is the 'glue' connecting the physical environment to habitat selection and social networks. Individually-based habitat selection and social network phenotypes are predicted to collectively influence fitness.

7.6 References

Angulo E, Luque GM, Gregory SD, Wenzel JW, Bessa-Gomes C, Berec L, Courchamp F. 2017. Allee effects in social species. J Anim Ecol. 87(1):47–58. doi:10.1111/1365-2656.12759.

Angulo E, Rasmussen GS a, Macdonald DW, Courchamp F. 2013. Do social groups prevent Allee effect related extinctions?: The case of wild dogs. Front Zool. 10(1):11. doi:10.1186/1742-9994-10-11.

Araújo MS, Bolnick DI, Layman CA. 2011. The ecological causes of individual specialisation. Ecol Lett. 14(9):948–958. doi:10.1111/j.1461-0248.2011.01662.x.

Barja I, Rosellini S. 2008. Does habitat type modify group size in roe deer and red deer under predation risk by Iberian wolves? Can J Zool. 86(3):170–176. doi:10.1139/Z07-129.

Bastille-Rousseau G, Schaefer JA, Mahoney SP, Murray DL. 2013. Population decline in semi-migratory caribou (*Rangifer tarandus*): intrinsic or extrinsic drivers? Can J Zool. 91(11):820–828. doi:doi:10.1139/cjz-2013-0154.

Berec L, Angulo E, Courchamp F. 2007. Multiple Allee effects and population management. Trends Ecol Evol. 22(4):185–191. doi:10.1016/j.tree.2006.12.002.

Bolnick DI, Yang LH, Fordyce JA, Davis JM, Svanbäck R. 2002. Measuring individual-level resource specialization. Ecology. 83(10):2936–2941.

Bourbeau-Lemieux A, Festa-Bianchet M, Gaillard JM, Pelletier F. 2011. Predator-driven component Allee effects in a wild ungulate. Ecol Lett. 14(4):358–363. doi:10.1111/j.1461-0248.2011.01595.x.

Bowman J, Ray JC, Magoun AJ, Johnson DS, Neil Dawson F. 2010. Roads, logging, and the large-mammal community of an eastern Canadian boreal forest. Can J Zool. 88(5):454–467. doi:10.1139/Z10-019.

Bradbury JW, Vehrencamp SL, Clifton KE. 2015. The ideal free antelope: foraging dispersions. Behav Ecol. 26(5):1303–1313. doi:10.1093/beheco/arv078.

Cantor M, Maldonado-Chaparro AA, Beck KB, Hanja B, Carter GG, He P, Hillemann F, Klarevas-Irby JA, Ogino M, Papageorgiou D, et al. 2020. The importance of individual-to-society feedbacks in animal ecology and evolution. bioarXiv.

Chamaillé-Jammes S, Fritz H, Valeix M, Murindagomo F, Clobert J. 2008. Resource variability, aggregation and direct density dependence in an open context: The local regulation of an African elephant population. J Anim Ecol. 77(1):135–144. doi:10.1111/j.1365-2656.2007.01307.x.

Cresswell W. 1998. Variation in the strength of interference competition with resource density in blackbirds, *Turdus merula*. Oikos. 81(1):152–160. doi:10.2307/3546477.

Dickie M, McNay RS, Sutherland GD, Cody M, Avgar T. 2020. Corridors or risk? Movement along, and use of, linear features vary predictably among large mammal predator and prey species. J Anim Ecol. 89(2):623–634. doi:10.1111/1365-2656.13130.

Dostie MJ, Lusseau D, Bonnell T, Clarke PMR, Chaplin G, Kienzle S, Barrett L, Henzi SP. 2016. Proof of principle: the adaptive geometry of social foragers. Anim Behav. 119:173–178. doi:10.1016/j.anbehav.2016.07.011.

Duparc A, Garel M, Marchand P, Dubray D, Maillard D, Loison A. 2019. Revisiting the functional response in habitat selection for large herbivores: A matter of spatial variation in resource distribution? Behav Ecol. 30(6):1725–1733. doi:10.1093/beheco/arz141.

Farine DR, Garroway CJ, Sheldon BC. 2012. Social network analysis of mixed-species flocks: Exploring the structure and evolution of interspecific social behaviour. Anim Behav. 84(5):1271–1277. doi:10.1016/j.anbehav.2012.08.008.

Fowler CW. 1981. Density dependence as related to life history strategy. Ecology. 62(3):602–610.

Fretwell SD, Lucas HLJ. 1969. On territorial behaviour and other factors influencing habitat distribution in birds. Acta Biotheor. 19(1):16–36. doi:10.1007/BF01601953.

Fryxell JM, Mosser A, Sinclair ARE, Packer C. 2007. Group formation stabilizes predator–prey dynamics. Nature. 449(October):1041–1044. doi:10.1038/nature06177.

Gerard JF, Bideau E, Maublanc ML, Loisel P, Marchal C. 2002. Herd size in large herbivores: Encoded in the individual or emergent? Biol Bull. 202(3):275–282.

Gregory SD, Bradshaw CJ., Brook BW, Courchamp F. 2010. Limited evidence for the demographic Allee effect from numerous species across taxa. Ecology. 91(7):2151–2161.

Hamilton WD. 1971. Geometry for the selfish herd. J Theor Biol. 31(2):295–311. doi:10.1016/0022-5193(71)90189-5.

He P, Maldonado-Chaparro AA, Farine DR. 2019. The role of habitat configuration in shaping social structure: a gap in studies of animal social complexity. Behav Ecol Sociobiol. 73:9.

Higashi M, Yamamura N. 1993. What determines animal group size? Insider-outsider conflict and its resolution. Am Nat. 142(3):553–563.

Hinde RA. 1976. Interactions, relationships and social structure. Man. 11(1):1–17.

Holbrook JD, Olson LE, DeCesare NJ, Hebblewhite M, Squires JR, Steenweg R. 2019. Functional responses in habitat selection: clarifying hypotheses and interpretations. Ecol Appl. 29(3):1–15. doi:10.1002/eap.1852.

Jacobs A. 2010. Group cohesiveness during collective movements: Travelling apart together. Behav Processes. 84(3):678–680. doi:10.1016/j.beproc.2010.03.004.

Jacoby DMP, Freeman R. 2016. Emerging network-based tools in movement ecology. Trends Ecol Evol. 31:301–314. doi:10.1016/j.tree.2016.01.011.

James ARC, Boutin S, Hebert DM, Rippin AB. 2004. Spatial Separation of Caribou From Moose and Its Relation To Predation By Wolves. J Wildl Manage. 68(4):799–809. doi:10.2193/0022-541x(2004)068[0799:ssocfm]2.0.co;2.

Jolles JW, King AJ, Killen SS. 2019. The role of individual heterogeneity in collective animal behaviour. Trends Ecol Evol. 35:278–291. doi:10.1016/j.tree.2019.11.001.

Kramer AM, Dennis B, Liebhold AM, Drake JM. 2009. The evidence for Allee effects. Popul Ecol. 51:341–354. doi:10.1007/s10144-009-0152-6.

Lafontaine A, Drapeau P, Fortin D, Gauthier S, Boulanger Y, St-Laurent M. 2019. Exposure to historical burn rates shapes the response of boreal caribou to timber harvesting. Ecosphere. 10(5):e02739. doi:10.1002/ecs2.2739.

Lafontaine A, Drapeau P, Fortin D, St-Laurent M-H. 2017. Many places called home: the adaptive value of seasonal adjustments in range fidelity. J Anim Ecol. 86:624–633. doi:10.1111/1365-2656.12645.

Leclerc M, Vander Wal E, Zedrosser A, Swenson JE, Kindberg J, Pelletier F. 2016. Quantifying consistent individual differences in habitat selection. Oecologia. 180:697–705. doi:10.1007/s00442-015-3500-6.

Lewis KP, Mahoney SP. 2014. Caribou survival, fate, and cause of mortality in Newfoundland: a summary and analysis of the patterns and causes of caribou survival and mortality in Newfoundland during a period of rapid population decline (2003-2012). Tech Bull No 009, Sustain Dev Strateg Sci Gov Newfoundl Labrador, St John's, NL.

Lima SL. 1995. Back to the basics of anti-predatory vigilance: the group-size effect. Anim Behav. 49:11–20.

Lima SL, Dill LM. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. Can J Zool. 68(4):619–640. doi:10.1139/z90-092.

Manly BFJ, McDonald LL, Thomas DL, McDonald TL, Erickson WP. 2002. Resource selection by animals: statistical design and analysis for field studies. 2nd Editio. Dordrecht: Kluwer Academic.

McLellan BN, Serrouya R, Wittmer HU, Boutin S. 2010. Predator-mediated Allee effects in multi-prey systems. Ecology. 91(1):286–292.

Menz CS, Carter AJ, Best EC, Freeman NJ, Dwyer RG, Blomberg SP, Goldizen AW. 2020. Higher sociability leads to lower reproductive success in female kangaroos. R Soc Open Sci. 7:200950.

Moody AL, Houston AI. 1996. Interference and the ideal free distribution: Models and tests. Behav Ecol. 7(4):379–386. doi:10.1093/beheco/7.4.379.

Moorcroft PR. 2012. Mechanistic approaches to understanding and predicting mammalian space use: recent advances, future directions. J Mammal. 93(4):903–916. doi:10.1644/11-MAMM-S-254.1.

Van Moorter B, Rolandsen CM, Basille M, Gaillard J-M. 2016. Movement is the glue connecting home ranges and habitat selection. J Anim Ecol. 85:21–31. doi:10.1111/1365-2656.12394.

Morris DW. 1987. Tests of density-dependent habitat selection in a patchy environment. Ecol Monogr. 57(4):269–281.

Morris DW. 2003. Toward an ecological synthesis: a case for habitat selection. Oecologia. 136(1):1–13. doi:10.1007/s00442-003-1241-4.

Morris DW. 2011. Adaptation and habitat selection in the eco-evolutionary process. Proc R Soc B. 278(1717):2401–2411. doi:10.1098/rspb.2011.0604.

Muller Z, Cantor M, Cuthill IC, Harris S. 2018. Giraffe social preferences are context dependent. Anim Behav. 146:37–49. doi:10.1016/j.anbehav.2018.10.006.

Mumma MA, Soulliere CE, Mahoney SP, Waits LP. 2014. Enhanced understanding of predator-prey relationships using molecular methods to identify predator species, individual and sex. Mol Ecol Resour. 14(1):100–108. doi:10.1111/1755-0998.12153.

Mysterud A, Ims RA. 1998. Functional responses in habitat use: availability influences relative use in trade-off situations. Ecology. 79:1435–1441.

Nathan R, Getz WM, Revilla E, Holyoak M, Kadmon R, Saltz D, Smouse PE. 2008. A movement ecology paradigm for unifying organismal movement research. Proc Natl Acad Sci. 105(49):19052–19059. doi:10.1073/pnas.0800375105.

Nielsen SE, Shafer ABA, Boyce MS, Stenhouse GB. 2013. Does Learning or Instinct Shape Habitat Selection? PLoS One. 8(1):1–5. doi:10.1371/journal.pone.0053721.

Parker GA, Sutherland WJ. 1986. Ideal free distributions when individuals differ in competitive ability: phenotype-limited ideal free models. Anim Behav. 34(4):1222–1242. doi:10.1016/S0003-3472(86)80182-8.

Peignier M, Webber QMR, Koen EL, Laforge MP, Robitaille AL, Vander Wal E. 2019. Space

use and social association in a gregarious ungulate: Testing the conspecific attraction and resource dispersion hypotheses. Ecol Evol. 9:5133–5145. doi:10.1002/ece3.5071.

Pelletier F, Clutton-Brock T, Pemberton J, Tuljapurkar S, Coulson T. 2007. The evolutionary demography of ecological change: Linking trait variation and population growth. Science (80-). 315(5818):1571–1574. doi:10.1126/science.1139024.

Pinter-Wollman N. 2015. Persistent variation in spatial behavior affects the structure and function of interaction networks. Curr Zool. 61(1):98–106.

Pinter-Wollman N, Fiore SM, Theraulaz G. 2017. The impact of architecture on collective behaviour. Nat Ecol Evol. 1:1–2. doi:10.1038/s41559-017-0111.

Prichard AK, Parrett LS, Lenart EA, Caikoski JR, Joly K, Person BT. 2020. Interchange and Overlap Among Four Adjacent Arctic Caribou Herds. J Wildl Manage.:1–15. doi:10.1002/jwmg.21934.

Prima MC, Duchesne T, Fortin A, Rivest LP, Drapeau P, St-Laurent MH, Fortin D. 2019. A landscape experiment of spatial network robustness and space-use reorganization following habitat fragmentation. Funct Ecol. 33(9):1663–1673. doi:10.1111/1365-2435.13380.

Rayl ND, Fuller TK, Organ JF, Mcdonald JE, Otto RD, Bastille-Rousseau G, Soulliere CE, Mahoney SP. 2015. Spatiotemporal variation in the distribution of potential predators of a resource pulse: Black bears and caribou calves in Newfoundland. J Wildl Manage. 79(7):1041–1050. doi:10.1002/jwmg.936.

Schaefer JA, Mahoney SP. 2013. Spatial dynamics of the rise and fall of caribou (*Rangifer tarandus*) in Newfoundland. Can J Zool. 91(11):767–774. doi:10.1139/cjz-2013-0132.

Schmidt KA, Johansson J, Betts MG. 2015. Information-Mediated Allee Effects in Breeding Habitat Selection. Am Nat. 186(6):162–171. doi:10.1086/683659.

Shaw AK. 2020. Causes and consequences of individual variation in animal movement. Mov Ecol. 8(1):1–12. doi:10.1186/s40462-020-0197-x.

Snyder-Mackler N, Burger JR, Gaydosh L, Belsky DW, Noppert GA, Campos FA, Bartolomucci A, Yang YC, Aiello AE, O'Rand A, et al. 2020. Social determinants of health and survival in humans and other animals. Science (80-). 368(6493). doi:10.1126/SCIENCE.AAX9553.

Spiegel O, Leu ST, Sih A, Bull CM. 2016. Socially interacting or indifferent neighbours? Randomization of movement paths to tease apart social preference and spatial constraints. Methods Ecol Evol. 7:971–979. doi:10.1111/2041-210X.12553.

Spiegel O, Sih A, Leu ST, Bull CM. 2018. Where should we meet? Mapping social network interactions of sleepy lizards shows sex-dependent social network structure. Anim Behav. 136:207–215. doi:10.1016/j.anbehav.2017.11.001.

Stamps JA, Krishnan VV, Willits NH. 2009. How different types of natal experience affect habitat preference. Am Nat. 174(5):623–630. doi:10.1086/644526.

Stephens PA, Sutherland WJ, Freckleton RP. 1999. What is the Allee effect? Oikos. 87(1):185–190.

Stewart FEC, Service CF, Canada NR, W BR. 2020. Boreal Caribou Can Coexist with Natural but Not Industrial Disturbances. J Wildl Manage.:1–10. doi:10.1002/jwmg.21937.

Strandburg-Peshkin A, Farine DR, Couzin ID, Crofoot MC. 2015. Shared decision-making drives collective movement in wild baboons. Science (80-). 348(6241):1358–1361.

Sueur C, King AJ, Conradt L, Kerth G, Lusseau D, Mettke-Hofmann C, Schaffner CM, Williams L, Zinner D, Aureli F. 2011. Collective decision-making and fission-fusion dynamics: A conceptual framework. Oikos. 120(11):1608–1617. doi:10.1111/j.1600-0706.2011.19685.x.

Sutherland WJ. 1983. Aggregation and the "Ideal Free" Distribution. J Anim Ecol. 52(3):821–828.

Vors LS, Boyce MS. 2009. Global declines of caribou and reindeer. Glob Chang Biol. 15(11):2626–2633. doi:10.1111/j.1365-2486.2009.01974.x.

Webber QMR, Laforge MP, Bonar M, Robitaille AL, Hart C, Zabihi-Seissan S, Wal E Vander. 2020. The ecology of individual differences empirically applied to space-use and movement tactics. Am Nat. 196(1). doi:10.1086/708721.

Webber QMR, Vander Wal E. 2018. An evolutionary framework outlining the integration of individual social and spatial ecology. J Anim Ecol. 87(1):113–127. doi:10.1111/1365-2656.12773.

Webber QMR, Vander Wal E. 2019. Trends and perspectives on the use of animal social network analysis in behavioural ecology: a bibliometric approach. Anim Behav. 149:77–87. doi:10.1016/j.anbehav.2019.01.010.

Weir JN, Mahoney SP, McLaren B, Ferguson SH. 2007. Effects of Mine Development on Woodland Caribou Rangifer Tarandus Distribution. Wildlife Biol. 13(1):66–74. doi:10.2981/0909-6396(2007)13[66:eomdow]2.0.co;2.

Williams CK, Lutz RS, Applegate RD. 2003. Optimal group size and northern bobwhite coveys. Anim Behav. 66(2):377–387. doi:10.1006/anbe.2003.2215.

Wittmer HU, Sinclair ARE, Mclellan BN, Wittmer HU, Sinclair ARE, Mclellan BN. 2005. The Role of Predation in the Decline and Extirpation of Woodland Caribou. Oecologia. 144(2):257–267. doi:10.1007/s00442-005-0055-y.

SUPPLEMENTARY MATERIALS

The following sections are supplementary materials that correspond to primary thesis chapters. Note, Chapter 1 and 7 do not have any supplementary material, so supplementary section ‘S1’ begins with Chapter 2.

S1 Supplementary materials – Chapter 2

Table S2.1 Glossary of terms

Term	Definition	Reference
Animal Model	A form of mixed model where an individual's phenotype is partitioned into a linear sum of different effects. The model includes an individual breeding value (i.e., pedigree) as a random effect and the additive genetic variance is estimated based on the comparison of phenotypes of relatives.	Charmantier, Garant & Kruuk (2014)
Animal personality	Consistent individual differences in behaviour across time and contexts.	Sih et al. (2004)
Behavioural hypervolume	The *n*-dimensional volume occupied by an individual, population or community in behavioural trait-space. Note, Pruitt et al. (2016) has had an authorship removal correction (Pruitt et al. 2016b).	Pruitt et al. (2016)
Behavioural syndrome	Inter-individual correlations between behaviour across time and contexts.	Sih et al. (2004)
Behavioural reaction norm	Set of behavioural phenotypes that an individual produces in a given set of environments. Genotypes or individuals show phenotypic plasticity if their reaction norm is non-horizontal.	Dingemanse et al. (2010)
Betweenness	The total number of shortest paths among nodes in a network. Paths reflect routes of connections that can be followed on a graph from one node to another.	Brent (2015)
Biophysical environment	The combination biotic and abiotic (e.g. vegetation, topography, elevation, climate etc.) characteristics which cumulatively represent spatial and temporal environmental variation.	-
Centrality	The extent to which an individual node occupies a position that is important to the structure of the social network. Examples of centrality include eigenvector centrality, degree, and betweenness (see definitions in Glossary).	Croft, Ruxton & Krause (2008)
Coarse-grained habitat selection	Typical for theory-based research on habitat selection where organisms are free to occupy discrete habitats, e.g., A, B, or C.	McLoughlin et al. (2010)

Degree	The number of edges joined to a node.	Croft, Ruxton & Krause (2008)
Ecological niche	Environmental requirements needed for a species to subsist without immigration. Volume in the environmental space that permits positive growth.	Trainor & Schmitz (2014)
Eigenvector centrality	The sum of an individual's direct and indirect connections, which is proportional to the centralities of individuals to which it is connected.	Csárdi & Nepusz (2006)
Fine-grained habitat selection	Typical for empiricists interested in quantifying habitat selection where an organism's use or occupancy of a site is defined by a multivariate set of continuous and categorical resources or resource covariates (applies to the RSF concept).	McLoughlin et al. (2010)
Graph strength	Total weight of the edges connected to a node, combining the degree of a node with the weight of all its edges.	Croft, Ruxton & Krause (2008)
Habitat	A spatially bounded area, with a subset of physical and biotic conditions, within which the density of interacting individuals, and at least one of the parameters of population growth, is different than in adjacent subsets.	Morris (2003)
Indirect genetic effects (IGE)	Genetic effects that occur any time an individual phenotype is causally influenced by the genotype of one or more conspecifics, typically through social interactions.	Moore, Brode & Wolf (1997)
Repeatability	A standardized measure of variation in average phenotype across individuals, mathematically defined as the proportion of phenotypic variance explained by differences between individuals.	McLoughlin et al. (2010)
Resource selection function (RSF)	Defined by characteristics measured on resource units such that its value for a unit is proportional to the probability of that unit being used by an organism.	Manly *et al. (*2002)
Social cognition	Suite of skills that allow an animal to recognize conspecifics, remember relationships and, perhaps, to attribute mental states to these animals. The degree of social cognition an organism is capable of ranges widely across taxa.	Seyfarth & Cheney (2015)

Social phenotype	An individual social trait which, may or may not be repeatable and heritable. A social phenotype can include, but is not limited to, social network metrics.	-
Social environment	Social life of an individual (or group of individuals) described by social interactions.	Saltz et al. (2016)
Social interaction	An action of one individual directed toward another or affecting the behaviour of another.	Whitehead (2008)
Social niche	Set of social environments in which the focal individual has non-zero inclusive fitness.	Saltz et al. (2016)
Social structure	The nature, quality, and patterning of the relationships among members of a population or group. This includes group size, composition, and individual measures of sociality as well as assortment of individuals within a group, or population, based on behavioural traits, body size, demographic structure, or other intrinsic factors.	Hinde (1976)
Spatial cognition	Perception and use of boundary and landmark information that reflect the experience, knowledge, goals, and motivation of the organism. Perception and cognition account for two ways in which spatial information is gained: 1) the emergence of strategies via salient spatial information; and 2) changes during lifespan development and experience.	Dolins & Mitchell (2010)
Spatial phenotype	Predilection for specific resource, such as food or habitat. To meet criteria for personality this predilection should be repeatable across time.	-

Table S2.2: Summary of technologies which could be used to quantify aspects of the socioecological environment. We delineate technologies as either continuous or discrete, where continuous (or near continuous) technologies are those which collect spatial and/or social data through time and space, while discrete technologies are those which collect spatial and/or social data at either discrete locations or during discrete time-frames. We provide positive and negative comments, as well as, when possible, empirical social network analysis (SNA) and resource selection function (RSF) examples for each technology. We also provide justification for combining two technologies to improve the quality of the data with respect to quantifying aspects of the socioecological environment. We avoid including prohibitive monetary costs or logistic difficulties in our 'negatives' section because all technologies listed below are expensive and provide some degree of logistic complications (during both data collection and management).

Tracking technology	Tracking status	Positive	Negative	SNA Example	RSF Example	Justification for combination
Visual observation	Near continuous[1]	Detailed observations of social associations and/or locations	Observations typically restricted to diurnal periods	Drewe (2010)	N/A	GPS collars provide near-continuous relocation data
GPS radio collars or tags	Near continuous[2]	Detailed spatial relocation data	Sampling intervals are infrequent (typically every 1-2 hour fixes)	Godfrey et al. (2014)[3]	Boyce et al. (2015)	Proximity collars improve quality of social interaction data[4]
Proximity collars or tags	Continuous	Detailed social interaction data	Directionality of association unknown; spatial location unknown	Vander Wal, Yip & McLoughlin (2012)	Ossi et al. (2016)	GPS radio collars provide near-continuous relocation data[4]

Light-based geolocators	Continuous	Detailed spatial relocation data	Social interactions unknown	N/A	Vandeperre et al. (2016)[5]	Proximity tags improve quality of social interactions data; PIT-tags improve social co-occurrence at specific location
VHF radio telemetry	Discrete	Potential for detailed spatial relocation data	Social interactions difficult to ascertain; labour intensive to collect spatial relocation data	Perkins et al. (2009)	Johnson, Seip & Boyce (2004)[6]	Proximity tags improve quality of social interaction data
Passive Integrated Transponders (PIT-tags)	Discrete	Detailed co-occurrence at specific location (e.g., roosts, nests, or feeders)	Restricted to specific location (e.g., roosts, feeders)	Aplin et al. (2012)	N/A	Addition of any technology with detailed spatial relocation data
Passive acoustic array	Discrete	Detailed site co-occurrence and general movement patterns within array	Restricted to species with distinct vocal calls and individuals in area of array	Mennill et al. (2012)[7]	N/A	Addition of any technology with detailed spatial relocation data
Passive telemetry array	Discrete	Detailed site co-occurrence and general movement patterns within array, useful for cryptic species	Restricted to individuals within area of array, not ideal for ranging, migratory, or nomadic species	Jacoby, Papastamatiou & Freeman (2016)	N/A	Addition of any technology with detailed spatial relocation data
Passive camera array (photo/video)	Discrete	Detailed co-occurrence and movement within area of array,	Restricted to individuals within area of array, not ideal for ranging,	Fisher, Rodríguez-Muñoz & Tregenza (2016)	N/A	Addition of any technology with detailed spatial relocation data

	useful for cryptic species	migratory, or nomadic species

[1] Dependent on animal observation protocol.
[2] Dependent on fix-rate: short intervals between fixes are continuous, long intervals are near continuous.
[3] 10-minute fix-rate.
[4] GPS radio collars/tags and proximity collars/tags may be the most effective combination to quantify near continuous spatial occurrence and continuous social interactions.
[5] Among the first studies to use light-based geolocators to quantify RSFs.
[6] VHF technology near obsolete for RSFs, GPS technology is now standard protocol.
[7] Study does not explicitly quantify social networks using passive acoustic arrays but the authors advocate for their use

S2 Supplementary materials – Chapter 3

Newfoundland, as well as Fogo Island, has a humid-continental climate and persistent precipitation throughout the year. The dominant land types consisted of coniferous and mixed forests of balsam fir (*Abies balsamea*), black spruce (*Picea mariana*) and white birch (*Betula papyrifera*), as well as bogs, lakes, and barren rock. Fogo Island (237 km^2) is situated ~12 km off the northeastern coast of Newfoundland (49º40'0'' N, 54º11'0'' W). Unlike many of the other herds in Newfoundland (Bastille-Rousseau et al. 2013), caribou on Fogo Island have a relatively stable population that has not declined in recent years. In addition, caribou on Fogo Island are sedentary and do not display any migratory or long-distance movements.

We deployed GPS collars on 26 adult female caribou (n = 72 caribou-years) in three phases. In spring 2016, 2017 and 2018, collars were deployed on individual caribou (n = 13 in 2016, n = 11 in 2017, n = 1 in 2018). After two years, new collars were deployed, thus animals collared in spring 2016 were re-collared in spring 2018 (n = 11). Collars continuously collected data throughout the year and were programmed to collect locations every two hours. For all analyses, we restricted locations to only include relocations from the first 75 days of each year (1 January–16 March). Prior to analyses, we removed all erroneous and outlier GPS locations following Bjørneraas et al. (2010). We also removed individuals with collar failure during the study period (n = 16 caribou-years) or individuals that swam to nearby adjacent islands (n = 3 caribou-years). After data screening, 24 adult female caribou (50 caribou-years) were used to generate annual social networks and 21 of these individuals (38 caribou-years) were used to assess patterns of movement, space use, and social behaviour in winter.

Table S3.1 Summary of three integrated step selection models run for each caribou-year. Note, the covariates included in model 1 were included in all subsequent models. Step length and nearest neighbour distance were log-transformed, and turn angle was cosine transformed. We also denote whether a variable was included in the model at the 'start' (e.g., t_2 from Figure 3.2) or 'end' (e.g., t_3 from Figure 3.2) from a given step.

Model	Covariates
Core	Habitat (end) + Time of day (start) : Turn angle + Time of day (start) : Step length
Nearest neighbour	Core + Nearest neighbour distance (end) + Turn angle : Nearest neighbour distance (start) + Step length : Nearest neighbour distance (start) + Habitat (end) : Nearest neighbour distance (end)
Simple ratio index	Core + Nearest neighbour distance (end) + Turn angle : Nearest neighbour distance (start) + Step length : Nearest neighbour distance (start) + Habitat (end) : Nearest neighbour distance (end) + Turn angle : Simple ratio index + Step length : Simple ratio index + Habitat (end) : Simple ratio index

Table S3.2: Summary of Utilization Distribution Overlap Index (UDOI) for caribou social community across three years. Note, although some communities did not overlap, these were generally restricted to communities that contained a single individual (communities 5 and 6 in 2018 and community 3 in 2019; see Table 3.1 of the main text for details).

Comparison	Year	UDOI
Communities 1–2	2017	0.689
Annual average	**2017**	**0.689**
Communities 1–2	2018	0.857
Communities 1–3	2018	0.357
Communities 2–3	2018	0.373
Communities 1–4	2018	0.445
Communities 2–4	2018	0.482
Communities 3–4	2018	0.830
Communities 1–5	2018	0
Communities 2–5	2018	0
Communities 3–5	2018	0
Communities 4–5	2018	0
Communities 1–6	2018	0.408
Communities 2–6	2018	0.436
Communities 3–6	2018	0.844
Communities 4–6	2018	0.980
Communities 5–6	2018	0
Annual average	**2018**	**0.40 ± 0.35**
Communities 1–2	2019	0.286
Communities 1–3	2019	0
Communities 2–3	2019	0
Annual average	**2019**	**0.095 ± 0.16**
Total average	**All years**	**0.37 ± 0.34**

Table S3.3: Summary of ΔAIC values for each caribou-year. For the Fogo Island herd, the model that included the simple ratio index (SRI) and nearest neighbour distance (NN) was ranked highest for all 34 caribou-years for which we ran a model that included the SRI, and for the additional four models that we were unable to include SRI, the NN distance model ranked highest.

ID	Year	Best Model	ΔAIC		
			Core model	Nearest neighbour model	SRI model
FO2016002	2017	SRI	2248.17	1248.47	0
FO2016002	2018	SRI	1897.58	991.03	0
FO2016002	2019	SRI	3173.93	2135.18	0
FO2016003	2017	NN	1298.93	0	–
FO2016004	2017	SRI	2958.17	1069.49	0
FO2016004	2018	SRI	3219.09	1855.79	0
FO2016005	2017	SRI	3048.21	1317.33	0
FO2016005	2018	SRI	3459.83	1330.03	0
FO2016005	2019	SRI	2469.97	1274.18	0
FO2016008	2017	SRI	3722.16	1368.19	0
FO2016009	2019	SRI	3403.91	1712.90	0
FO2016010	2017	SRI	3778.12	1502.61	0
FO2016010	2018	SRI	3589.44	1625.28	0
FO2016012	2017	SRI	3718.37	1368.64	0
FO2016012	2018	SRI	3961.40	1654.12	0
FO2016013	2017	SRI	1291.23	914.43	0
FO2016013	2018	SRI	1819.29	956.05	0
FO2016013	2019	SRI	2759.80	1623.43	0
FO2016014	2017	SRI	2320.28	1928.86	0
FO2016014	2018	SRI	2308.28	1808.96	0
FO2016014	2019	SRI	2400.15	1980.00	0
FO2016015	2017	SRI	3223.50	1161.54	0
FO2016015	2019	SRI	2337.92	1509.66	0
FO2017001	2018	NN	46.78	0	–
FO2017001	2019	SRI	2660.63	1377.98	0
FO2017003	2018	NN	2814.27	0	–
FO2017004	2018	SRI	2582.34	1566.34	0
FO2017006	2018	SRI	3787.27	1611.41	0
FO2017007	2018	SRI	3441.19	1072.84	0
FO2017008	2018	SRI	3699.46	1441.05	0
FO2017008	2019	SRI	3609.27	2011.80	0
FO2017009	2018	SRI	3718.76	1584.54	0

FO2017009	2019	SRI	3662.53	2006.56	0
FO2017012	2018	SRI	3968.08	1402.44	0
FO2017012	2019	SRI	2388.72	1537.20	0
FO2017014	2018	SRI	3584.12	1490.04	0
FO2017014	2019	NN	14.68	0	–
FO2018002	2019	SRI	3623.31	1553.53	0

Table S3.4: Summary of integrated step selection analysis covariates for models that included nearest neighbour distance and the simple ratio index as covariates (N = 34 caribou-years). Note, proportion of positive ß refers to the number of individual models where the ß coefficient for a given covariate in the model was positive and population ß's are summarized with 95% confidence interval around the mean. For covariates with 95% confidence intervals that do not overlap zero we provide a brief interpretation of the result.

Covariate	Proportion positive ß	ß	Lower CI	Upper CI	Interpretation
Forest	0.71	2.54	1.012	4.068	Individuals select forest habitat relative to open-moving habitat.
Lichen	0.79	1.694	1.038	2.350	Individuals select lichen habitat relative to open-moving habitat.
Turn angle : Time of day (day)	0.44	–0.035	–0.091	0.021	–
Turn angle : Time of day (night)	0.41	–0.038	–0.101	0.024	–
Step length : Time of day (day)	1.00	1.491	1.242	1.740	Longer step lengths during the day compared to available step lengths during the day.
Step length : Time of day (night)	1.00	1.322	1.080	1.563	Longer step lengths during the night compared to available step lengths during the night.
Turn angle : Simple ratio index	0.62	–0.002	–0.02	0.015	–
Step length : Simple ratio index	1.00	0.483	0.442	0.523	Longer step lengths when the focal individual has a high dyadic SRI value with their nearest neighbour.
Turn angle : Nearest neighbour distance (start)	0.59	0.006	–0.006	0.018	–
Step length : Nearest neighbour distance (start)	0.97	0.171	0.134	0.208	Longer step lengths when individuals are further from their nearest neighbour.

Forest : Simple ratio index	1.00	1.105	0.683	1.526	Individuals select to be nearest individuals with which they share a higher dyadic SRI value when selecting forest habitat compared to open-moving habitat.
Lichen : Simple ratio index	1.00	1.015	0.876	1.155	Individuals select to be nearest individuals with which they share a higher dyadic SRI value when selecting lichen habitat compared to open-moving habitat.
Forest : Nearest neighbour distance (start)	0.74	0.235	0.086	0.385	Individuals are further from their nearest neighbour when selecting forest habitat.
Lichen : Nearest neighbour distance (start)	0.97	0.464	0.369	0.559	Individuals are further from their nearest neighbour when selecting lichen habitat.
Nearest neighbor distance	0.00	–1.19	–1.309	–1.074	Individuals are close to nearest neighbours.

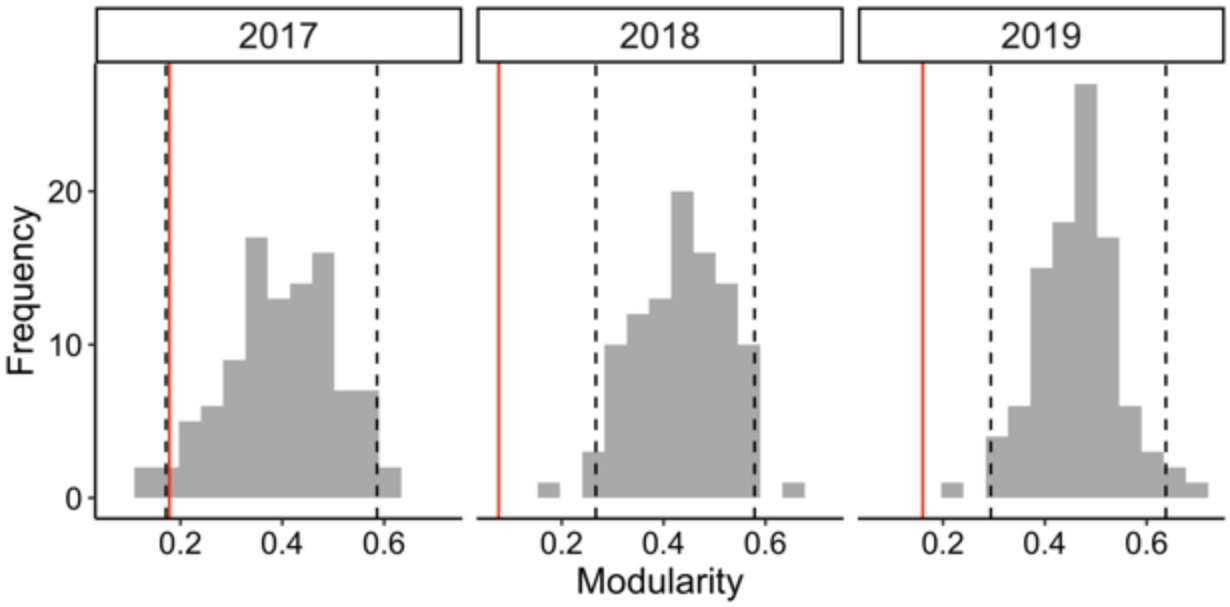

Figure S3.1: Comparison of observed modularity values (vertical red line) to the distribution of modularity values generated from null models in each year (95% confidence intervals are represented in each year by dashed black lines). In all years, observed modularity values were lower than the null distribution suggesting social associations among individuals in different social communities were more likely than expected by chance.

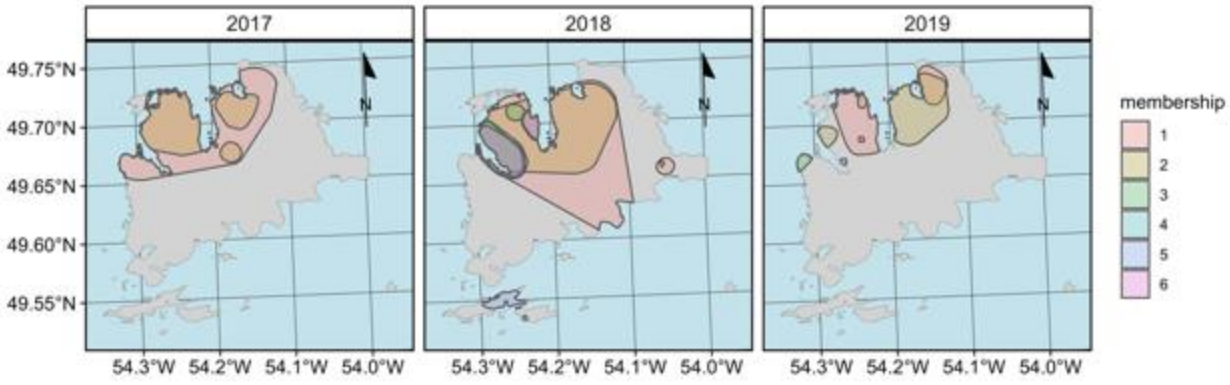

Figure S3.2: 95% kernel density estimates for Fogo Island social communities (2017–2019). Note, community overlap was relatively high in all years (Table S3.2). Communities are super-imposed over Fogo Island for contextualization.

S3 Supplementary materials – Chapter 4

Figure S4.1: Comparison of caribou foraging in lichen barrens (Panel A) and artificially enhanced habitat (Panel B). Photos were screen captured from focal observation videos recorded on 21 November 2019 (lichen barrens) and 5 November 2019 (artificially enhanced habitat).

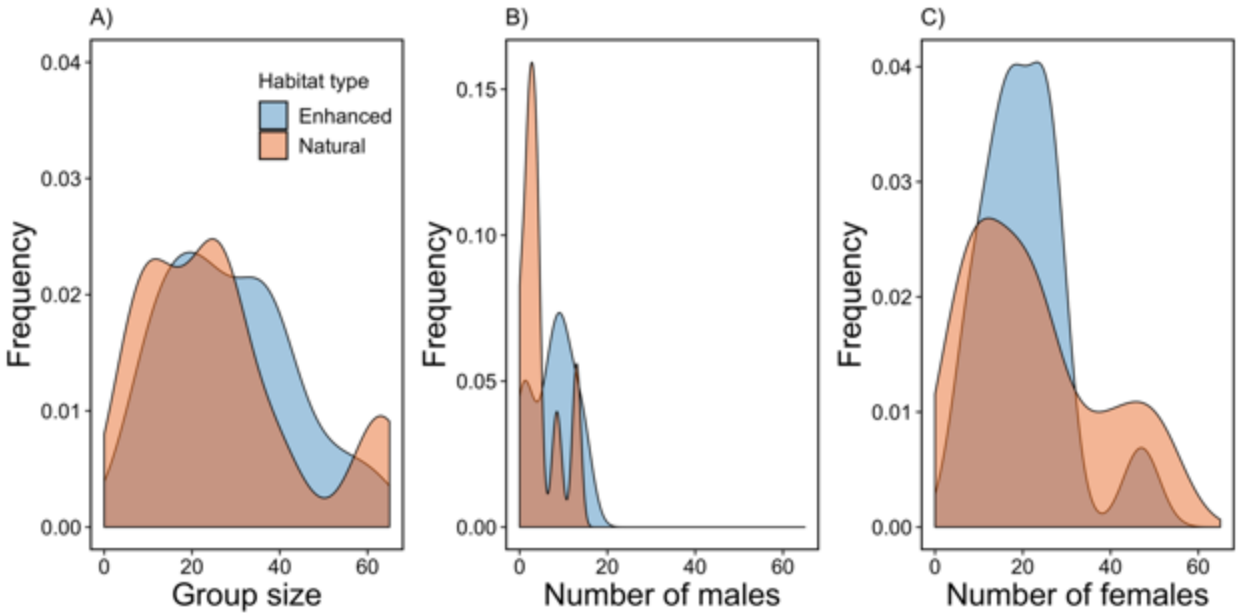

Figure S4.2: A) Distribution of group size in enhanced (blue, n = 32) and natural (orange, n = 40) habitat types as well as B) number of males and C) number of females in each group in enhanced and natural habitat types.

Table S4.1: Summary of model selection using Akaike Information Criteria (AIC) for two model sets testing the effects of various predictors on aggression and harassment behaviour of caribou. The marginal R2 ($R2_M$) value is the variance explained by fixed effects and conditional R2 ($R2_C$) is the variance explained by random effects. The first model includes video and group identity as random effects and the second model includes group identity as a random effect.

Prediction	Model	ΔAIC	Log likelihood	$R2_C$	$R2_M$	Distribution
P2a, P2b, P3a, P3b, and P3c	Frequency of aggression ~ habitat * group size + habitat * sex + behavior * sex + duration + year	–	–160.6	0.18	0.19	Negative Binomial
		7.75	–166.5	0.66	0.74	Poisson
P4a, P4b, and P4c	Frequency of male harassment ~ habitat * group size + habitat * sex ratio + duration + year	–	–53.5	0.015	0.019	Negative Binomial
		9.35	–59.2	0.68	0.87	Poisson

S4 Supplementary Materials – Chapter 5

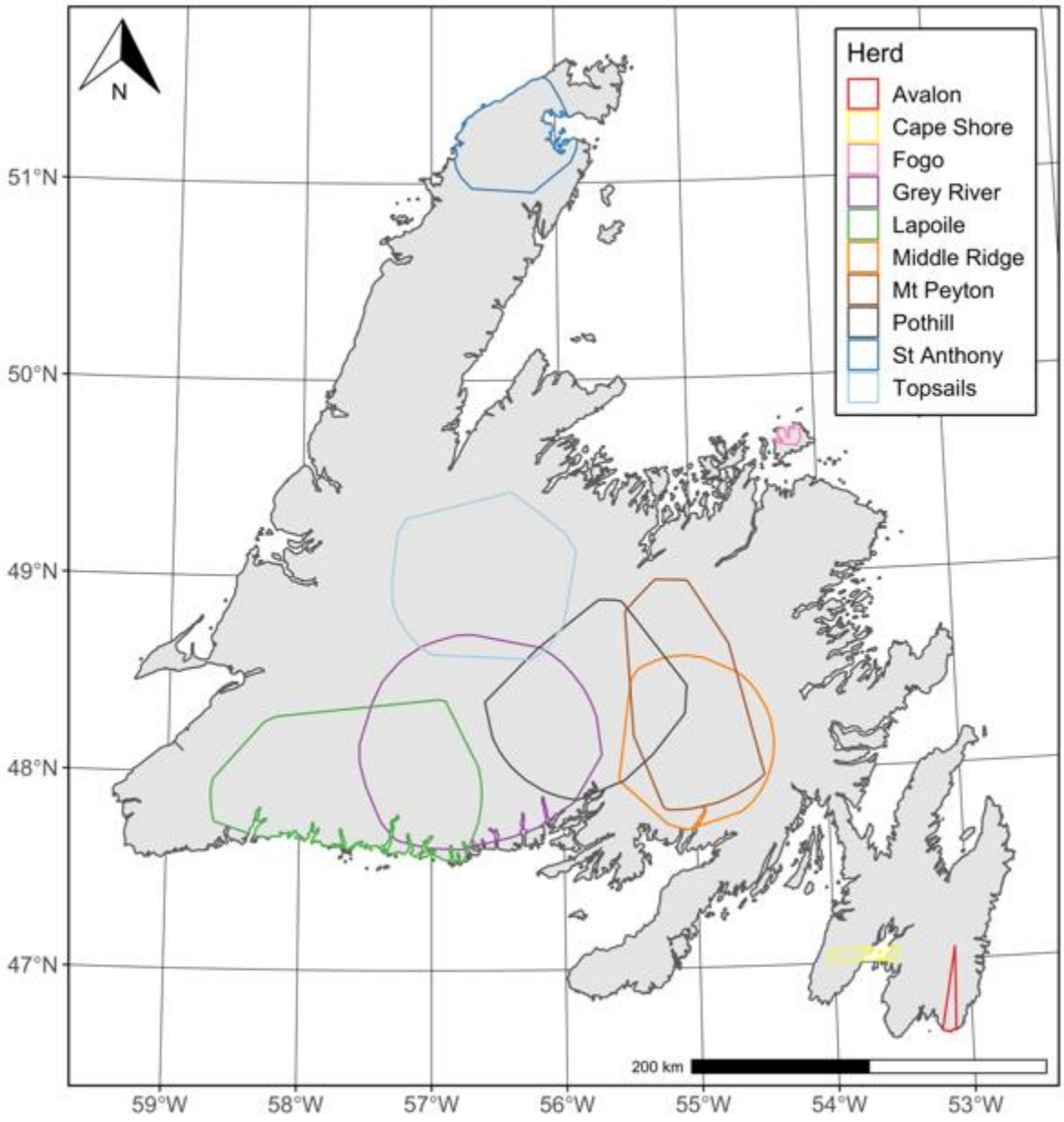

Figure S5.1: Locations of ten Newfoundland caribou herds monitored for group size.

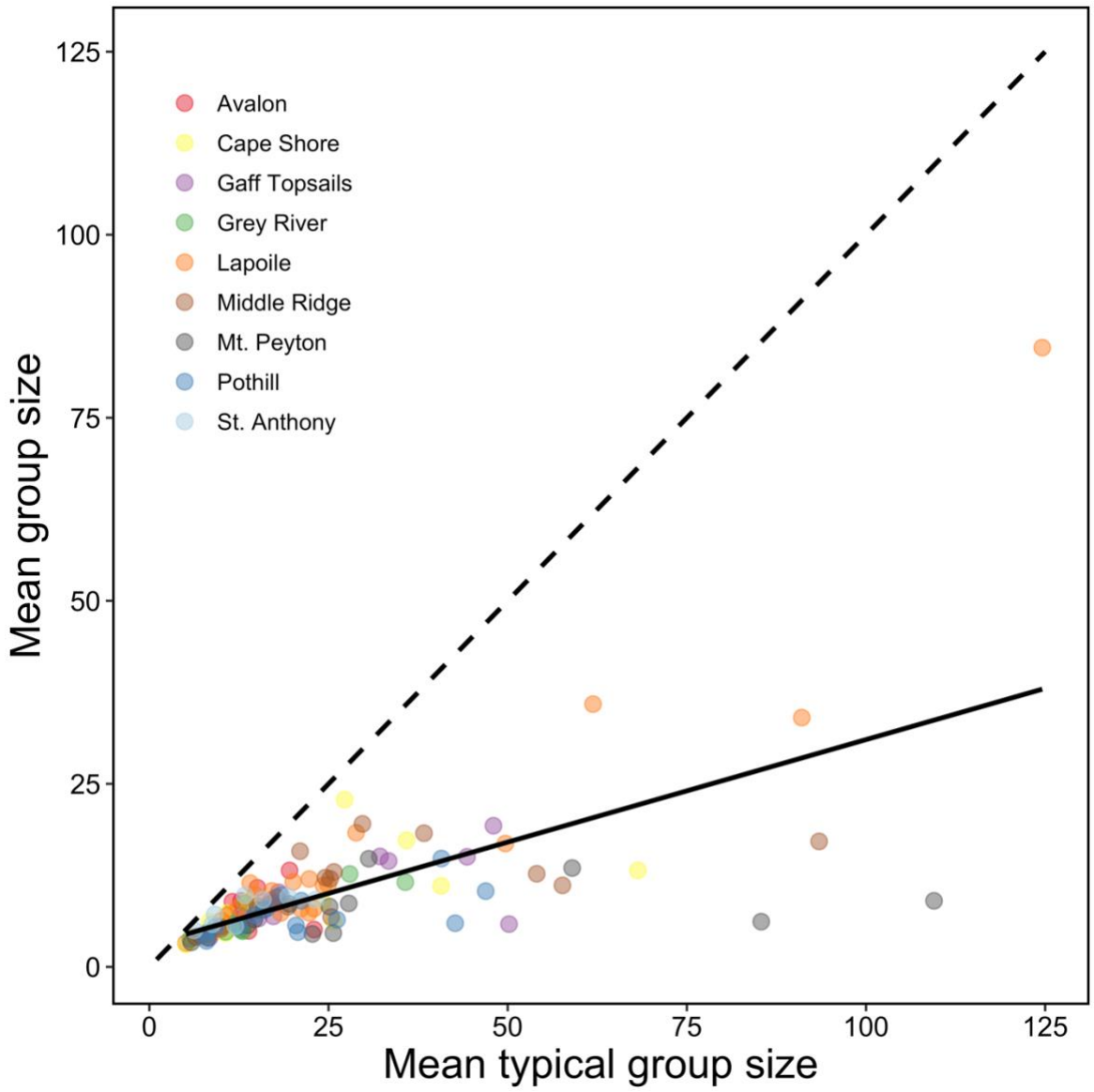

Figure S5.2: correlation between mean group size and mean typical group size for nine caribou (*Rangifer tarandus*) herds in Newfoundland (Pearson's $r = 0.67$, $p < 0.0001$). The dashed line represents the 1:1 relationship, while the solid line represents the linear regression relationship between mean and typical group size.

Table S5.1: Published reports of *Rangifer tarandus* group size as a function of whether a given study assessed differences in season, habitat, or density. In cases where mean or typical group size is approximated we estimated the average based on figures presented in text or calculated mean based on summary statistics for years or sites.

Study	Herd and region	Data collection method and number of years or seasons	Total population size	No. records of group size	Mean or typical group size (range, if included)	Comparison of group size		
						Season	Habitat	Density
Duquette and Klein (1987)	Porcupine Herd, Alaska and Yukon	Focal observations, 2 years (1982–83)	NR	NR	129 (8–393)[M]	No	No	No
Heard and Ouellet (1994)	Southampton Island, Northwest Territories	Annual aerial or snowmobile surveys (1978–91)	1,200–13,700	2,036	~11.0[T]	No	No	Yes
Stuart-Smith et al. (1997)	Northeastern Alberta	Monthly aerial surveys (1991–94)	7.7 per 100km^2	NR	~3.5[M]	Yes	No	No
Rettie and Messier (1998)	Churchill River Upland and Mid-Boreal Lowland, Saskatchewan	Aerial surveys throughout the year (1992–94)	NR	299	2.0 (1–18)[T]	Yes	No	No
Barten et al. (2001)	Wrangell St. Elias National Park, Alaska	Aerial surveys during calving (1994–95)	NR	NR	~8.1[M]	Yes, within-season	No	No
Mathisen et al. (2003)	Hjertind Reindeer District, Norway	Focal observation (1997–98)	700–800	NR	32 (max 300) [M]	No	No	No
Reimers et al. (2006)	Forolhogna, Norway	Focal observation (1996)	1,700–1,800	NR	126 (4–700) [M]	Yes	No	No
Weir et al. (2007)	Lapoile herd, Newfoundland and Labrador	Aerial surveys throughout the year (1985–91)	NR	NR	~10.4[M]	Yes	No	No
McLellan et al. (2010)	Banff National Park, British Columbia	Aerial surveys in summer (1984–2006)	~0–600	2,099	3.8[M]	No	No	Yes
Tennenhouse et al. (2011)	Kutuharju Field Reindeer Research Station, Finland	Focal observations (1996–2008)	NR	NR	~14.6[M]	No	No	No

Reimers et al. (2011)	Svalbard	Focal observation (2006)	181	NR	2.4 (1–11) [M]	No	No	No
Reimers et al. (2012)	Rondane, Hardangervidda, Forolhogna, Ottadalen North and South, and Norefjell-Reinsjøfjell herds, Norway	Video recordings and focal observation	0.5–1.5 per km^2	NR	~391[M]	No	No	No
L'Italien et al. (2012)	Kutuharju Field Reindeer Research Station, Finland	Focal observations (1996–2005)	~100	NR	NR[2]	No	No	No
Weckerly et al. (2014)	Adak Island, Alaska	Focal observations (2011–12)	~2,900	54	~15.7 (1–161)[M]	No	No	No
Body et al. (2014)	Kutuharju Field Reindeer Research Station, Finland	Focal observations (2011)	45	NR	NR[2]	No	No	No
Uccheddu et al. (2015)	Kutuharju Field Reindeer Research Station, Finland	Focal observations (1997–2012)	29–118	NR	13.8 (1–24)[M]	Yes, within-season	No	No
Body et al. (2015)	Kutuharju Field Reindeer Research Station, Finland	Focal observations (2009, 2011)	45–59	NR	NR[2]	Yes	No	No
Djaković et al. (2015)	Kutuharju Field Reindeer Research Station, Finland	Focal observations (2005)	NR	68	~11[T]	No	No	No
Jung et al. (2019)	Dehcho region, Northwest Territories	Aerial surveys in winter (2006–2016)	NR	456	5.5 (1–24)[T]	Yes, within-season	No	No

[M]: mean group size; [T]: typical group size; NR: not reported; [1]Sum of the number of females and males per group; [2]Group size calculated, but summary statistics not provided.

Table S5.2: Summary of model selection using Akaike Information Criteria (AIC) for models testing the effects of log-transformed population density on annual average group size for nine Newfoundland caribou herds separated into size categories. Herds were categorized into small (Avalon, Cape Shore, and Mt. Peyton), medium (Grey River, Gaff Topsails, Pot Hill, and St. Anthony), and large herds (Middle Ridge and La Poile) for analyses. Note, Gaussian distribution was used instead of Poisson for this model set because the response variable was mean group size as opposed to group size counts.

Model	Herd size	ΔAIC	Log likelihood	Model pseudo R^2	Distribution
Mean group size ~ log(density)	Small	–	–99.87	0.19	Negative binomial
Mean group size ~ log(density)	Small	–10.14	–105.05	0.83	Gaussian
Mean group size ~ log(density) + year + herd	Small	–11.56	–86.76	0.79	Negative binomial
Mean group size ~ log(density) + year + herd	Small	–19.29	–90.63	0.99	Gaussian
Mean group size ~ log(density)	Medium	–	–113.8	0.03	Negative binomial
Mean group size ~ log(density) + year + herd	Medium	–2.13	–97.83	0.75	Negative binomial
Mean group size ~ log(density) + year + herd	Medium	–7.86	–100.71	0.99	Gaussian
Mean group size ~ log(density)	Medium	–8.26	–117.9	0.22	Gaussian
Mean group size ~ log(density)	Large	–	–110.51	0.39	Negative binomial
Mean group size ~ log(density) + year + herd	Large	–7.85	–93.44	0.93	Negative binomial
Mean group size ~ log(density)	Large	–18.51	–119.77	0.99	Gaussian
Mean group size ~ log(density) + year + herd	Large	–20.29	–98.66	1.00	Gaussian

Table S5.3: Summary of model selection using Akaike Information Criteria (AIC) for models testing the effects of habitat (open or closed), season (calving or winter), and log-transformed population density on group size for nine Newfoundland caribou herds. Note, herds were separated into small (Avalon, Cape Shore, and Mt. Peyton), medium (Grey River, Gaff Topsails, Pot Hill, and St. Anthony), and large herds (Middle Ridge and La Poile) for analyses.

Model	Herd size	ΔAIC	Log likelihood	Model pseudo R^2	Distribution
Group size ~ habitat*log(density) + season*log(density) + year	Small	–	–251.7	0.31	Negative binomial
Group size ~ habitat*log(density) + season*log(density)	Small	–8.36	–258.9	0.09	Negative binomial
Group size ~ habitat*log(density) + season*log(density) + year	Small	–302.4	–403.9	0.75	Poisson
Group size ~ habitat*log(density) + season*log(density)	Small	–382.9	–447.2	0.31	Poisson
Group size ~ habitat*log(density) + season*log(density) + year	Medium	–	–515.7	0.51	Negative binomial
Group size ~ habitat*log(density) + season*log(density)	Medium	–25.8	–535.6	0.25	Negative binomial
Group size ~ habitat*log(density) + season*log(density) + year	Medium	–870.0	–951.7	0.99	Poisson
Group size ~ habitat*log(density) + season*log(density)	Medium	–1192.5	–1120.0	0.93	Poisson
Group size ~ habitat*log(density) + season*log(density) + year	Large	–	–897.7	0.45	Negative binomial
Group size ~ habitat*log(density) + season*log(density)	Large	–9.79	–907.6	0.38	Negative binomial
Group size ~ habitat*log(density) + season*log(density) + year	Large	–1345.5	–1571.5	0.97	Poisson

Group size ~ habitat*log(density) + season*log(density)	Large	–1549.2	–1678.3	0.94	Poisson

Table S5.4: Summary of model selection using Akaike Information Criteria (AIC) for models testing the effects of habitat and season on group size for Fogo Island caribou.

Model	ΔAIC	Log likelihood	Model pseudo R^2	Distribution
Group size ~ habitat*season	–	–1035.1	0.36	Negative binomial
Group size ~ habitat*season + year	–2.89	–1033.5	0.37	Negative binomial
Group size ~ habitat*season + year	–443.5	–1254.8	0.59	Poisson
Group size ~ habitat*season	–447.7	–1260.0	0.58	Poisson

S5 Supplementary Materials – Chapter 6

S6.1 Additional information on study area, data collection, and subjects

We studied adult female caribou (*Rangifer tarandus*) from six herds (Buchans, Grey River, La Poile, Middle Ridge, Pot Hill, and Topsails) on the Island of Newfoundland, Canada (Figure S1: 47°44'N, 52°38'W to 51°44'N, 59°28'W) between 2007–2013 (Table S6.1). Caribou (n = 127 individuals) were immobilized by a dart fired from a helicopter and outfitted with global positioning system (GPS) collars (Lotek Wireless Inc., Newmarket, ON, Canada, GPS4400M collars, 1,250 g). Collars were deployed on individual caribou for one to three years, but collars were often re-deployed on the same individuals for up to seven years. The Newfoundland and Labrador Department of Environment and Conservation captured and immobilized caribou by aerial darting from a helicopter with a mixture of carfentanil (12 mg/kg) and xylazine (0.2 mg/kg) or a mixture of ketamine (2 mg/kg) and xylazine (6 mg/kg) administered intramuscularly with a CO2-powered pistol (Palmer Cap-Chur Inc., Power Springs, Georgia). All collars were programmed to record locations every two hours, depending on herd, season, and year. Prior to analyses we screened telemetry data and removed all erroneous fixes (Bjørneraas et al. 2010). Animal capture and handling procedures conformed to guidelines established by the American Society of Mammalogists (Sikes and Mammalogists 2016).

Caribou ranges in Newfoundland comprise coniferous and mixed forest dominated by balsam fir (*Abies balsamea*), black spruce (*Picea mariana*), and white birch (*Betula papyrifera*), as well as bogs with stunted black spruce and tamarack (*Larix laricina*). Barren rock, lakes, and ponds are also common land features in Newfoundland. Caribou in Newfoundland have undergone drastic changes in abundance over the last 50 years, with low abundance from the 1950s to 1970s, followed by rapid growth in the 1980s and 1990s, and precipitous declines in the

2000s that persists to the present (Bastille-Rousseau et al. 2013). Broad-scale changes in population abundance were consistent across herds (Figure S6.2).

Table S6.1: Number of individual caribou (*Rangifer tarandus*) used for social network analysis and subsequent modeling in each year-by-season combination.

Year	Calving	Winter
2007	74	73
2008	62	62
2009	78	76
2010	74	74
2011	56	53
2012	34	34
2013	15	14

Table S6.2: Number of GPS relocations in each of eight habitat type separated by herd for 127 caribou (*Rangifer tarandus*) in Newfoundland, Canada between 2007–2013.

	Buchans	**Grey River**	**La Poile**	**Middle Ridge**	**Pot Hill**	**Topsails**	**All herds**
Wetland	32,797	25,886	29,992	72,134	17,269	48,145	226,223
Lichen barrens	32,147	31,912	33,248	32,692	23,757	26,255	180,011
Conifer scrub	12,439	21,244	14,237	26,237	35,942	22,580	132,679
Conifer forest	7,414	8,414	3,624	12,571	13,271	10,881	56,175
Water/ice	5,246	6,985	4,529	11,846	4,449	7,922	40,977
Rocky barrens	6,403	3,443	5,706	7,585	1,135	4,163	28,435
Mixed-wood forest	1,699	1,505	1,673	1,005	957	4,020	10,859
Deciduous forest	97	320	1690	23	61	616	2,807
Total	98,242	99,709	94,699	164,093	96,841	124,582	681,560

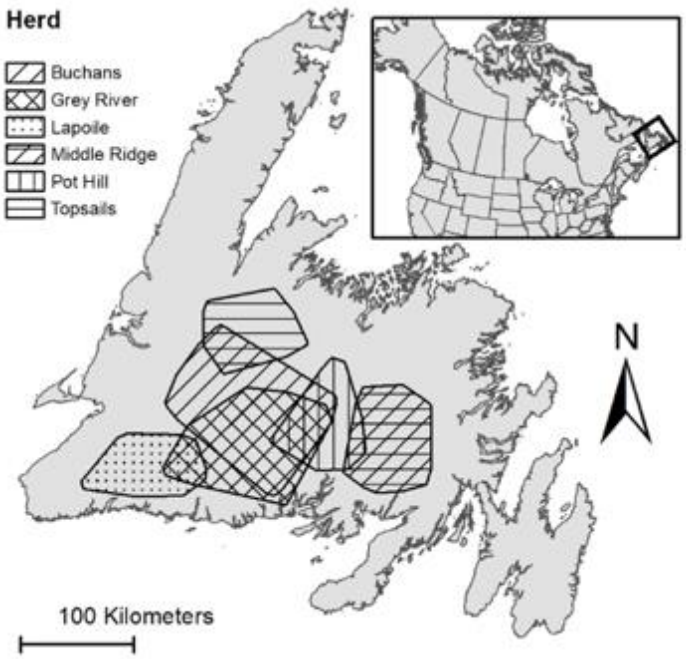

Figure S6.1: map of study area including six Newfoundland caribou (*Rangifer tarandus*) herds used for data collection between 2007–2013.

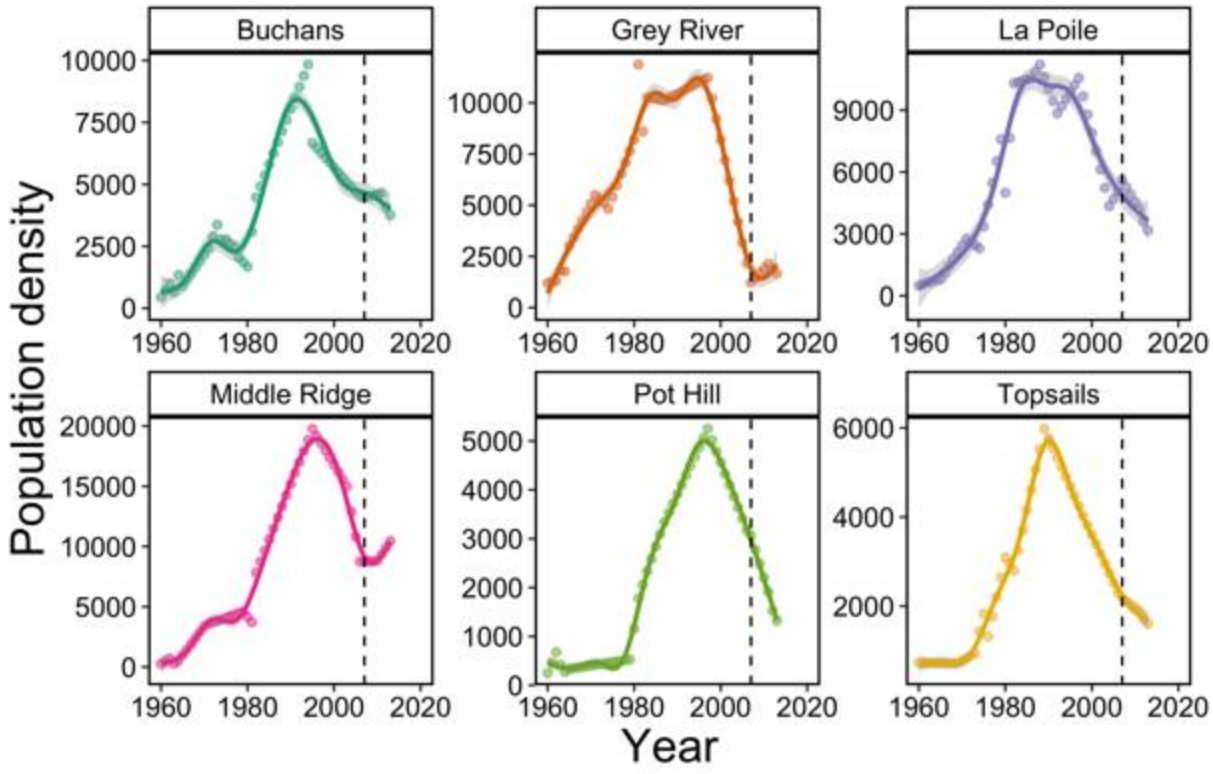

Figure S6.2: Herd-level changes in population density (i.e. abundance) between 1960 and 2013 for six caribou (*Rangifer tarandus*) herds in Newfoundland, Canada. For full details and description of population density data collection see Lewis & Mahoney (2014). Vertical dashed lines are placed at 2007, the date at which GPS collar data for this study were collected. From 2007 to 2013, Middle Ridge and Grey River herds increased in size, while Buchans, La Poile Pot Hill, and Topsails decreased in size. Note, y-axes differ for each herd for ease of interpretation.

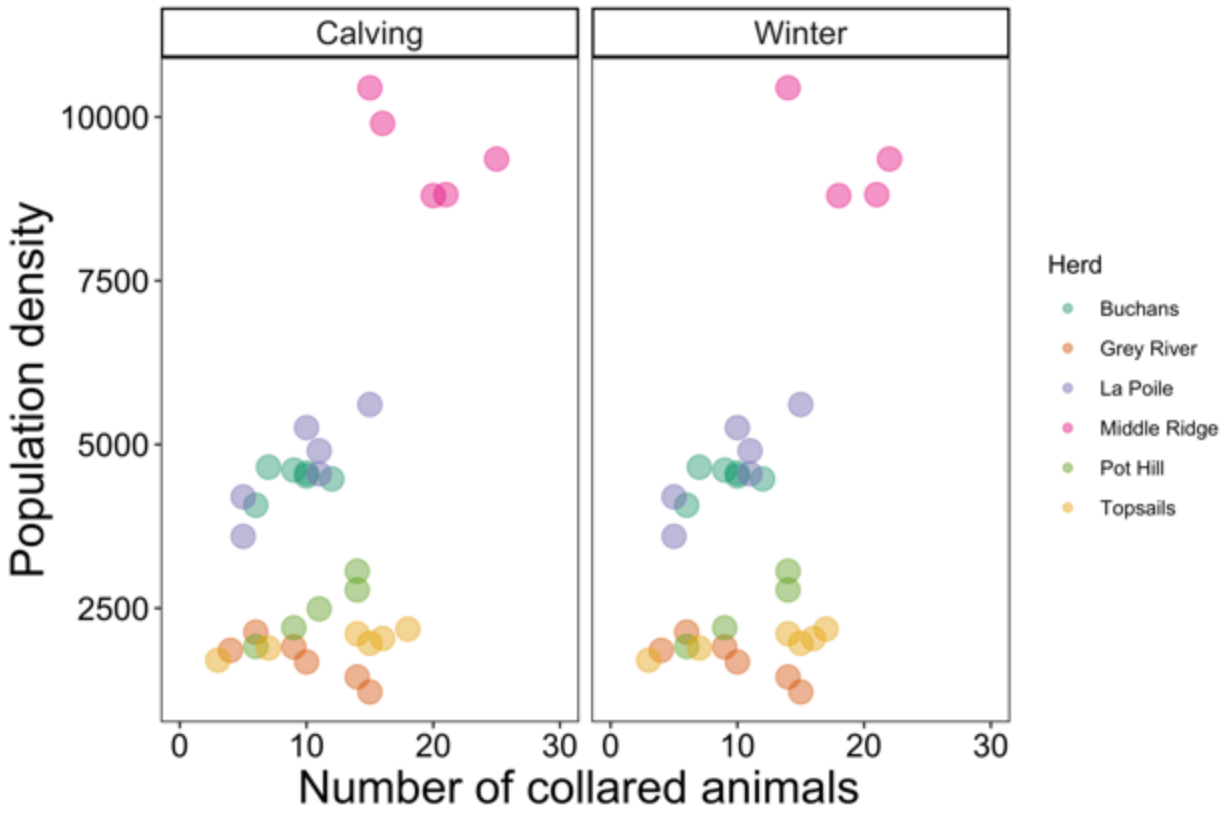

Figure S6.3: Number of collared animals in each herd at different herd density (measured here as abundance) between 2007 and 2013.

S6.2 Supplementary information on social networks and social network randomization

We used the *spatsoc* package (Robitaille et al. 2019) to generate proximity-based social networks (PBSN) from GPS telemetry data. As described in the main text, we applied the 'chain rule' to designate groups. Edges in each network were weighted based on the strength of association between dyads of caribou using the simple ratio index (Cairns and Schwager 1987), SRI:

$$SRI = \frac{x}{x + y_{AB} + y_A + y_B}$$

where x is the number of times individuals A and B were within 50 m of each other, y_A is the number of fixes from individual A when individual B did not have a simultaneous fix (i.e. within 5 minutes), y_B is the number of fixes from individual B when individual A did not have a simultaneous fix, and y_{AB} is the number of simultaneous fixes from individuals A and B that were separated by >50 m (Farine and Whitehead 2015). We constructed social networks with the *igraph* package in R (Csárdi and Nepusz 2006). Nodes in our networks represented individuals and edges represented associations between individuals based on the SRI.

Although we model the relationship between social strength, habitat specialization, and fitness using Bayesian inference (see main text, Tables S6.5–S6.8), we also developed data-stream permutations to assess the potential for non-random social structure through space and time (Farine 2017). Thus, separate from our Bayesian models, we generated null models based on GPS fixes to reduce potential for type II error typically associated with node-based permutations (Farine 2014). Following Spiegel et al. (2016), we re-ordered daily GPS movement trajectories for each individual while maintaining the temporal path sequence within each time block (e.g., day 1 and day 2 may be swapped). This technique is a robust network randomization procedure for GPS data because: 1) it maintains the spatial aspects of an individual's movement; 2) by randomizing movement trajectories of individuals independent of one another, temporal

dependencies of movement are decoupled (Spiegel et al. 2016). We repeated this procedure 100 times for each season-by-year social networks and re-calculated social strength at each iteration and compared observed social strength to the distribution of randomly generated values of strength (Figure S6.4).

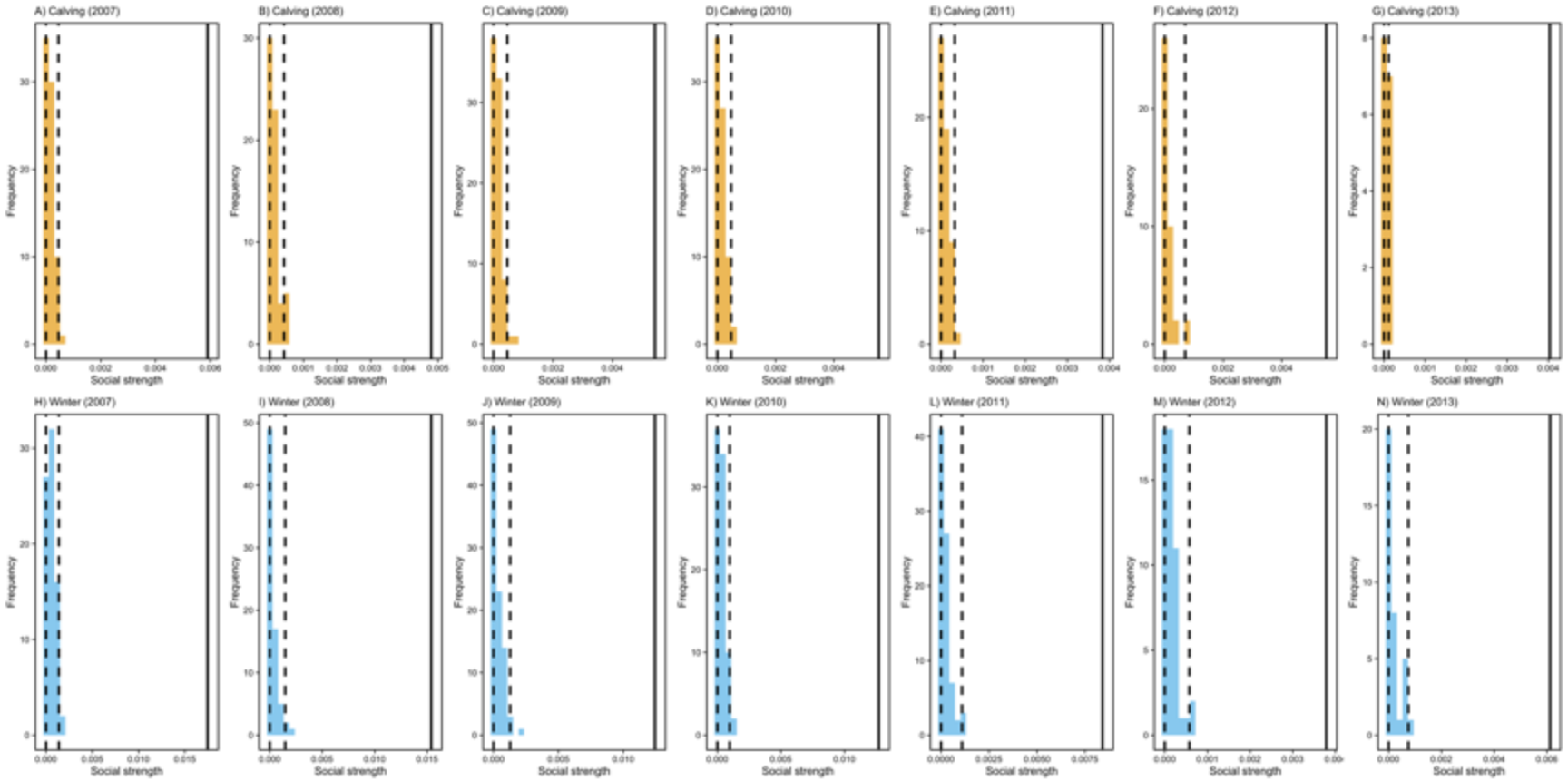

Figure S6.4: Comparison of observed social strength to a randomly generated distribution of social strength for caribou (*Rangifer tarandus*) in calving (Panels A-G) and winter (Panels H-N). The sold vertical line represent mean observed social strength for each season-by-year combination and the dashed lines represent 95% confidence intervals around the randomly generated distribution.

S6.3 Resource selection and habitat specialization

To ensure our measures of habitat specialization (i.e. proportional similarity index, see main text) were related to individual selection of specific habitats while accounting for habitat availability, we generated resource selection functions (RSFs). For each individual, we separated data into unique season-year combinations within which used locations were regressed against randomly generated locations within the home range (similar to a 3rd order analysis *sensu* Johnson 1980). RSFs produce a function that describes the relative probability of habitat selection across a landscape to quantify the habitat preference of a species. We used all GPS fixes from each individual's seasonal home-range to generate 95% MCP to define available habitat. We then modeled RSFs using a 1:10 ratio of used to available points within the MCP home range. Our goal with the RSF models was to quantify patterns of habitat selection for individuals in each of four habitat types. Explanatory variables in our RSFs included elevation and the proportion of four land-cover classes (lichen, rocky barrens, wetland, and conifer/scrub) within a 100 m buffer of each used and available location.

We then extracted coefficients from each individual-by-season-by-year RSF and compared them to habitat specialization measures for the same period time using a linear mixed effects model with a Gaussian distribution. The model included each habitat type (lichen, rocky barrens, wetland, and conifer/scrub) in an interaction with season as well as year as fixed effects and individual identity nested within herd as a random effect (Table S6.3). Habitat specialization was positively correlated with lichen selection, indicating that generalists tended to have stronger lichen selection, while habitat specialists tended to have weak selection or no preference for lichen (Table S6.3; Figure S6.5). In addition, there was a near-significant positive relationship between habitat specialization and selection for rocky barrens and wetland and no effect of

conifer (Table S6.3; Figure S6.5). These findings suggest that habitat generalists tend to select lichen more intensely compared to alternatives, while specialists tend to avoid or select lichens less intensely (Table S6.3; Figure S6.5), a result which also supports our finding that habitat specialists tend to be less social than generalists. Habitat specialists avoid lichen, which is commonly selected by most individuals, and specialize on other habitat types. We extracted marginal and conditional R^2 values to estimate the variance explained by the fixed effects (marginal) and random (conditional) effects (Nakagawa and Schielzeth 2013).

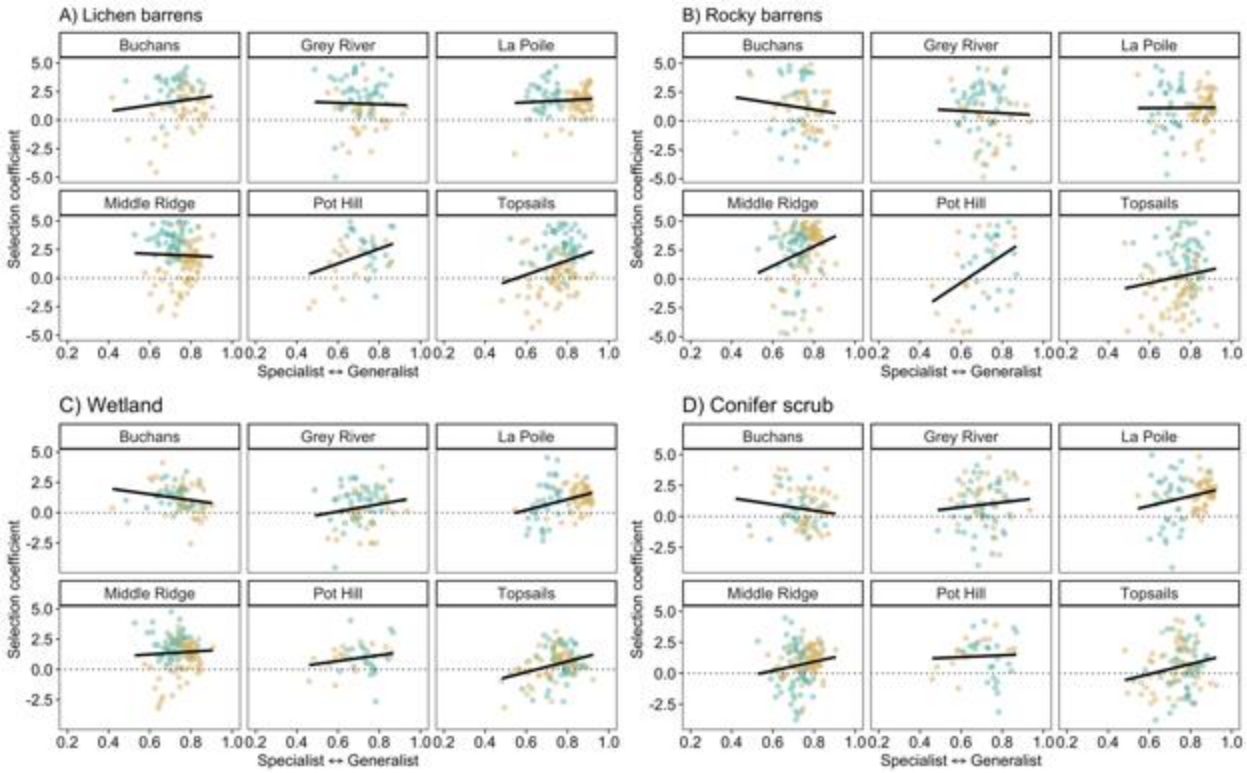

Figure S6.5: Comparison between habitat specialization (measured using the proportional similarity index, see main text) and habitat selection coefficients (extracted from resource selection functions) for four primary habitat types: A) lichen barrens; B) rocky barrens; C) wetland; and D) conifer scrub habitat types. Orange dots represent individual measures of habitat specialization and habitat selection during calving and green dots represent individuals during winter.

Table S6.3: Summary of linear mixed model testing the relationship between habitat specialization and habitat selection coefficients for lichen barrens, rocky barrens, wetland, and conifer scrub as well as season and year ($R2_m$ = 0.15 and $R2_c$ = 0.27). Individual identity was nested within herd as a random effect in the model.

Fixed effects	**β ± se**	**z-value**	**p-value**
Intercept	0.75 ± 0.01	78.0	**<0.001**
Lichen selection	0.01 ± 0.003	4.53	**<0.001**
Rocky barren selection	0.003 ± 0.002	1.85	0.064
Wetland selection	0.006 ± 0.003	1.83	0.067
Conifer selection	0.001 ± 0.002	0.43	0.66
Season (winter)[1]	–0.07 ± 0.01	–8.05	**<0.001**
Year[2]			
-2008	0.01 ± 0.011	1.09	0.27
-2009	–0.01 ± 0.011	–0.92	0.36
-2010	–0.008 ± 0.012	–0.65	0.51
-2011	0.006 ± 0.012	0.45	0.66
-2012	–0.02 ± 0.015	–1.07	0.29
-2013	–0.04 ± 0.02	–1.88	0.06
Random effects	**Variance ± SD**		
Herd:ID	0.00009 ± 0.009		
ID	0.001 ± 0.03		
Residual	0.006 ± 0.08		

[1]Reference category: calving.
[2]Reference category: 2007.

S6.4 Additional behavioural reaction norm methods

Behavioral reaction norms (BRNs) represent behavioral phenotypes expressed by individuals across an environmental gradient, where the BRN intercept reflects personality and the BRN slope reflects plasticity (Dingemanse et al. 2010). We used BRNs to evaluate repeatability and plasticity of social strength and habitat specialization as well as their relationship with fitness across a population density gradient. Models included social strength, habitat specialization, and reproductive success as co-response variables in a tri-variate Bayesian mixed model (package MCMCglmm: (Hadfield 2010)) as a function of mean-centered population density. To assess effects of individual (I) and environment (E) on our response variables we parameterized three models. First, we parameterized a global model which included all data (Table S6.4). Next, we separated our dataset based on individuals that experienced relatively high and relatively low density. Specifically, for the high density data subset we included the upper 75% quantile of density data and for the low density data subset we included the lower 25% quantile of density data. We then parameterized separate bivariate models at high and low density to investigate the relationship between habitat specialization and survival (Tables S6.5 and S6.6) and social strength and survival (Tables S6.7 and S6.8).

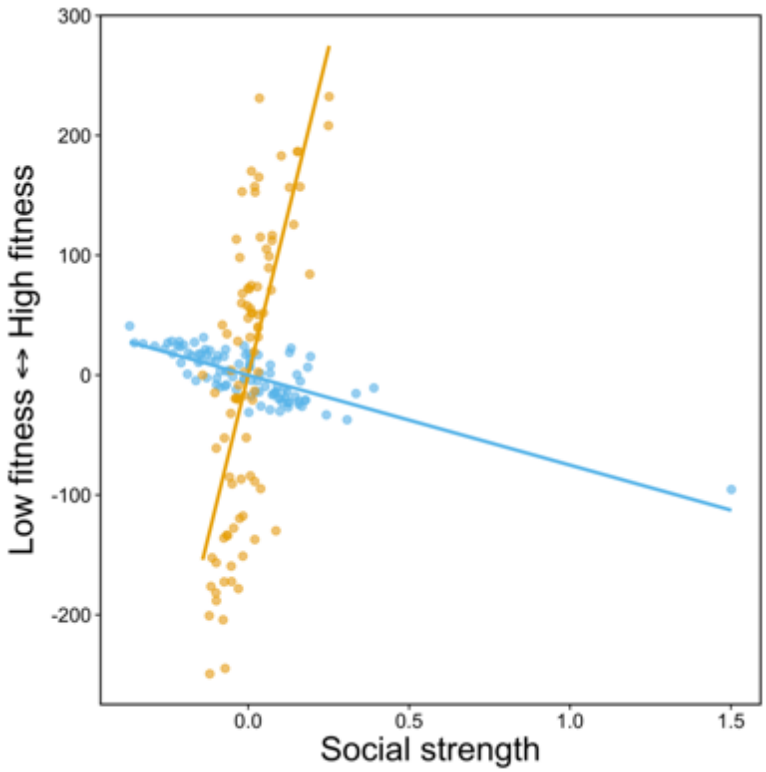

Figure S6.6: Phenotypic covariance between reproductive success and social strength at relatively high (orange points) and relatively low (blue points) population density for caribou (*Rangifer tarandus*, n = 127) in Newfoundland (see Table 6.3 in the main text for summary of phenotypic covariance estimates).

Table S6.4: Estimates for fixed effects are given for the global model with social strength, habitat specialization, and reproductive success (fitness) as co-response variables in a tri-variate Bayesian mixed model testing the effects of population density, herd, year (2007–2013), and season (winter or calving). 95% credible intervals are displayed in brackets for each posterior mean.

Variable	Social strength		Habitat specialization		Fitness	
	Posterior Mean	**MCMC p-value**	**Posterior Mean**	**MCMC p-value**	**Posterior Mean**	**MCMC p-value**
Social strength	–0.0001 (–0.01, 0.016)	0.98	–	–	–	–
Habitat specialization	–	–	0.02 (–0.06, 0.48)	0.11	–	–
Fitness	–	–	–	–	46.2 (–14.9, 125.2)	0.14
Density	–0.008 (–0.07, 0.06)	0.81	–0.17 (–0.25, –0.10)	**<0.001**	–1.32 (–15.7, 11.9)	0.85
Year[1]						
-2008	–0.11 (–0.23, 0.03)	0.11	–0.008 (–0.21, 0.18)	0.93	–9.13 (–50.7, 24.3)	0.59
-2009	–0.20 (–0.32, –0.08)	**0.001**	–0.30 (–0.49, –0.11)	**0.003**	21.5 (–15.9, 60.5)	0.22
-2010	–0.19 (–0.32, –0.63)	**0.003**	–0.45 (–0.65, –0.25)	**<0.001**	–17.5 (–57.8, 19.0)	0.32
-2011	–0.38 (–0.53, –0.23)	**<0.001**	–0.20 (–0.43, 0.01)	0.07	–5.8 (–46.8, 36.8)	0.76
-2012	–0.34 (–0.53, –0.15)	**<0.001**	–0.30 (–0.55, –0.05)	**0.01**	11.0 (–36.4, 64.1)	0.64
-2013	–0.56 (–0.81, –0.29)	**<0.001**	–0.61 (–1.01, –0.25)	**0.001**	–45.4 (–135.7, 21.3)	0.18
Herd[2]						
-Grey River	–0.39 (–0.56, –0.16)	0.005	–0.25 (–0.56, 0.07)	0.11	–39.8 (–132.8, 41.4)	0.31
-La Poile	0.007 (–0.19, 0.27)	0.95	0.16 (–0.15, 0.49)	0.33	–22.5 (–117.1, 52.9)	0.55
-Middle Ridge	0.13 (–0.75, 0.34)	0.19	0.19 (–0.09, 0.34)	0.18	20.4 (–53.7, 97.9)	0.47
-Pot Hill	–0.47 (–0.68, –0.26)	**<0.001**	–0.61 (–0.95, –0.28)	**<0.001**	–31.9 (–128.2, 48.9)	0.43
-Topsails	–0.13 (–0.35, 0.48)	0.17	0.06 (–0.23, 0.36)	0.67	1.79 (–76.8, 82.5)	0.97
Season						
-Winter[3]	0.06 (0.43, 0.73)	**<0.001**	0.003 (–0.09, 0.15)	0.65	1.45 (–20.1, 24.9)	0.89

[1] Reference category: 2007.
[2] Reference category: Buchans.
[3]Reference category: calving.

Table S6.5: Estimates for fixed effects are given for the low density model with habitat specialization and reproductive success (fitness) as co-response variables in a bi-variate Bayesian mixed model testing the effects of population density, herd, year (2007–2013), and season (winter or calving). 95% credible intervals are displayed in brackets for each posterior mean.

	Low density			
	Habitat specialization		**Fitness**	
Variable	**Posterior Mean**	**MCMC p-value**	**Posterior Mean**	**MCMC p-value**
Habitat specialization	–1.97 (–3.61, –0.48)	**0.01**	–	–
Fitness	–	–	74.8 (–50.6, 664.4)	0.80
Social strength	14.4 (2.27, 26.3)	0.01	–481 (–4642, 3795)	0.84
Density	–1.75 (–3.44, 0.009)	**0.05**	–84.8 (–736, 611)	0.79
Year[1]				
-2008	–0.02 (–0.65, 0.60)	0.96	34.4 (–226.6, 261.5)	0.77
-2009	–0.53 (–1.04, 0.03)	0.05	50.8 (–161.8, 256.3)	0.63
-2010	–0.50 (–1.07, 0.05)	0.08	–28.9 (–248.6, 174.8)	0.76
-2011	–0.43 (–1.01, 0.18)	0.16	–52.8 (–276.1, 180.8)	0.63
-2012	–0.11 (0.90, 0.69)	0.80	33.2 (–293.8, 332.6)	0.84
-2013	–0.69 (–1.48, 0.05)	0.07	–110.5 (–391.6, 156.5)	0.42
Herd[2]				
-Grey River	0.15 (–0.50, 0.80)	0.66	–131 (–337.7, 87.7)	0.21
-La Poile	0.87 (–0.28, 1.99)	0.13	–158.9 (–585, 242)	0.44
-Middle Ridge	0.93 (0.26, 1.64)	**0.01**	–12.8 (–246.9, 222.6)	0.92
-Pot Hill	–0.39 (–1.05, 0.27)	0.25	–8.83 (–301, 121.7)	0.41
Season				
-Winter[3]	0.56 (0.76, 1.09)	**0.04**	–89.3 (–303.5, 118.6)	0.40

[1] Reference category: 2007.
[2] Reference category: Buchans.
[3]Reference category: calving.

Table S6.6: Estimates for fixed effects are given for the high density model with habitat specialization and reproductive success (fitness) as co-response variables in a bi-variate Bayesian mixed model testing the effects of population density, herd, year (2007–2013), and season (winter or calving). 95% credible intervals are displayed in brackets for each posterior mean.

	High density			
	Habitat specialization		**Fitness**	
Variable	**Posterior Mean**	**MCMC p-value**	**Posterior Mean**	**MCMC p-value**
Habitat specialization	–1.51 (–2.30, –0.67)	0.001	–	–
Fitness	–	–	111 (–166, 382.8)	0.43
Social strength	9.18 (–4.98, 2.24)	0.20	–1651 (6137, 3059)	0.48
Density	0.26 (–0.05, 0.54)	0.09	9.94 (–90.6, 109.1)	0.84
Year[1]				
-2008	1.05 (0.42, 1.59)	**<0.001**	–18.5 (–211.1, 164.2)	0.85
-2009	0.22 (–0.45, 0.89)	0.52	136.6 (–98.8, 364.2)	0.23
-2010	1.51 (0.60, 2.43)	**0.001**	–162.5 (–453.6, 152.9)	0.27
-2011	2.23 (1.42, 2.99)	**<0.001**	–88.2 (–336.4, 152.1)	0.47
-2012	1.67 (0.98, 2.35)	**<0.001**	1.64 (–217.5, 216.9)	0.98
-2013	0.39 (–0.62, 1.53)	0.48	33.4 (–315.2, 413.3)	0.87
Herd[2]				
-Grey River	–1.56 (–2.41, –0.69)	**0.0005**	–65.9 (–342.6, 229)	0.64
-La Poile	0.11 (–0.46, 0.62)	0.69	–8.9 (–265.2, 107.7)	0.34
-Middle Ridge	–0.31 (–1.20, 0.59)	0.51	–109.6 (–440, 181)	0.47
-Pot Hill	0.52 (–0.21, 1.25)	0.17	–119.7 (–382.2, 136)	0.35
-Topsails	–0.98 (–1.83, –0.14)	**0.02**	144.3 (–150.3, 408.4)	0.29
Season				
-Winter[3]	0.91 (0.51, 1.23)	**<0.001**	15.8 (–121.3, 137.8)	0.80

[1] Reference category: 2007.
[2] Reference category: Buchans.
[3]Reference category: calving.

Table S6.7: Estimates for fixed effects are given for the low density model with social strength and reproductive success (fitness) as co-response variables in a bi-variate Bayesian mixed model testing the effects of population density, herd, year (2007–2013), and season (winter or calving). 95% credible intervals are displayed in brackets for each posterior mean.

	Low density			
	Social strength		**Fitness**	
Variable	**Posterior Mean**	**MCMC p-value**	**Posterior Mean**	**MCMC p-value**
Social strength	–2.03 (–3.98, –0.07)	**0.04**	–	–
Fitness	–	–	144.2 (–478.7, 772.3)	0.64
Habitat specialization	1.82 (0.44, 3.27)	**0.01**	–84.6 (–541.8, 337.6)	0.70
Density	–1.01 (–3.11, 1.10)	0.34	–72.0 (–715.8, 631.6)	0.83
Year[1]				
-2008	0.23 (–0.57, 0.96)	0.56	28.2 (–195.7, 276.2)	0.80
-2009	–0.54 (–1.17, 0.13)	0.11	47.9 (–162.1, 249.2)	0.66
-2010	–0.54 (–1.18, 0.13)	0.12	–32.5 (–239.65, 179.6)	0.75
-2011	–0.54 (–1.25, 0.20)	0.15	–54.5 (–280.6, 180.8)	0.63
-2012	–0.85 (–1.90, 0.14)	0.10	22.5 (–275.8, 340.5)	0.88
-2013	–0.60 (–1.47, 0.30)	0.19	–115.9 (–411.5, 151.6)	0.41
Herd[2]				
-Grey River	–0.71 (–1.34, –0.03)	0.03	–128.7 (–342.2, 97.4)	0.24
-La Poile	–0.38 (–1.67, 0.99)	0.57	–142.4 (–554.6, 274.7)	0.51
-Middle Ridge	0.19 (–0.54, 1.02)	0.62	–7.91 (–249.4, 230.8)	0.96
-Pot Hill	–0.22 (–0.96, 0.47)	0.55	–84.7 (–318.4, 128.4)	0.46
Season				
-Winter[3]	0.64 (–0.03, 1.33)	0.06	–88.3 (–293.6, 126.2)	0.39

[1] Reference category: 2007.
[2] Reference category: Buchans.
[3]Reference category: calving.

Table S6.8: Estimates for fixed effects are given for the high density model with social strength and reproductive success (fitness) as co-response variables in a bi-variate Bayesian mixed model testing the effects of population density, herd, year (2007–2013), and season (winter or calving). 95% credible intervals are displayed in brackets for each posterior mean.

	High density			
	Social strength		**Fitness**	
Variable	**Posterior Mean**	**MCMC p-value**	**Posterior Mean**	**MCMC p-value**
Social strength	0.26 (–0.91, 1.44)	0.67	–	–
Fitness	–	–	231.8 (–146.8, 627.7)	0.23
Habitat specialization	0.80 (–0.68, 2.28)	0.31	–250.7 (–767.9, 274.5)	0.34
Density	–0.03 (–0.35, 0.27)	0.85	14.8 (–89.4, 117.3)	0.77
Year[1]				
-2008	–1.00 (–1.59, –0.41)	**<0.001**	25.9 (–178.1, 210.6)	0.77
-2009	–0.71 (–5.66, –0.007)	**0.04**	159.0 (–56.6, 408.7)	0.15
-2010	–0.79 (–1.75, 0.18)	0.11	–126.4 (–459.3, 169.6)	0.41
-2011	–0.77 (–1.65, 0.09)	0.07	–23.3 (–300.8, 261.8)	0.86
-2012	–0.97 (–1.75, –0.26)	**0.01**	57.1 (–167.7, 292.3)	0.64
-2013	–1.43 (–2.51, –0.26)	**0.02**	7.16 (–287.7, 446.4)	0.69
Herd[2]				
-Grey River	–0.65 (–1.49, 0.32)	0.16	–109.1 (–409, 180.4)	0.45
-La Poile	–0.25 (–0.83, 0.29)	0.38	–86.6 (–271.1, 89.6)	0.35
-Middle Ridge	0.20 (–0.81, 1.15)	0.68	–128.5 (–437.2, 186.9)	0.41
-Pot Hill	–0.99 (–1.71, –0.29)	**0.008**	–97.9 (–352.3, 150.1)	0.44
-Topsails	–0.59 (–1.49, 0.29)	0.19	114.3 (–153.2, 404.3)	0.42
Season				
-Winter[3]	0.29 (–0.12, 0.72)	0.18	33.9 (–100.9, 171.7)	0.64

[1] Reference category: 2007.

[2] Reference category: Buchans.

[3]Reference category: calving.

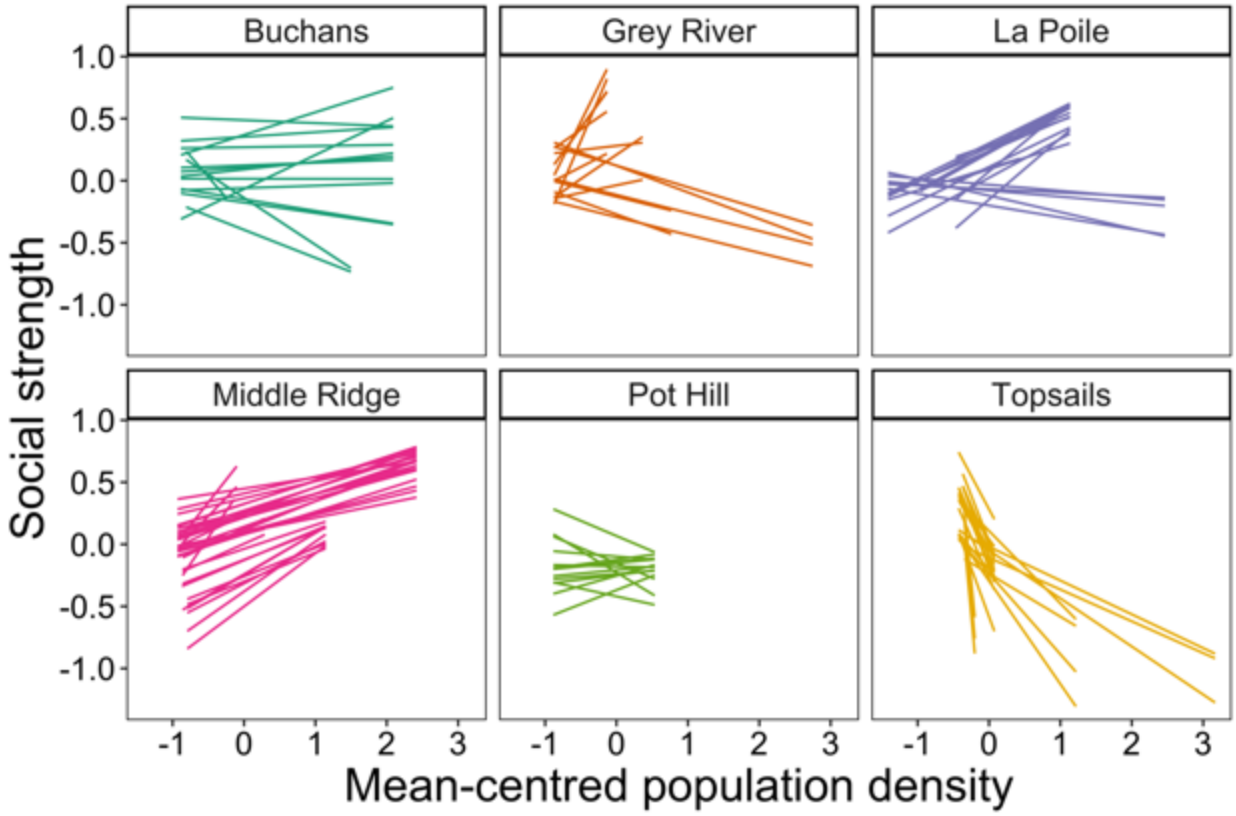

Figure S6.7: Behavioural reaction norms testing the relationship between social network strength and population density for caribou (*Rangifer tarandus*; n = 127) in six herds in Newfoundland. Each line represents an individual behavioural response to changes in population density and crossing of lines represents individual differences in plasticity (i.e., an individual-environment interaction).

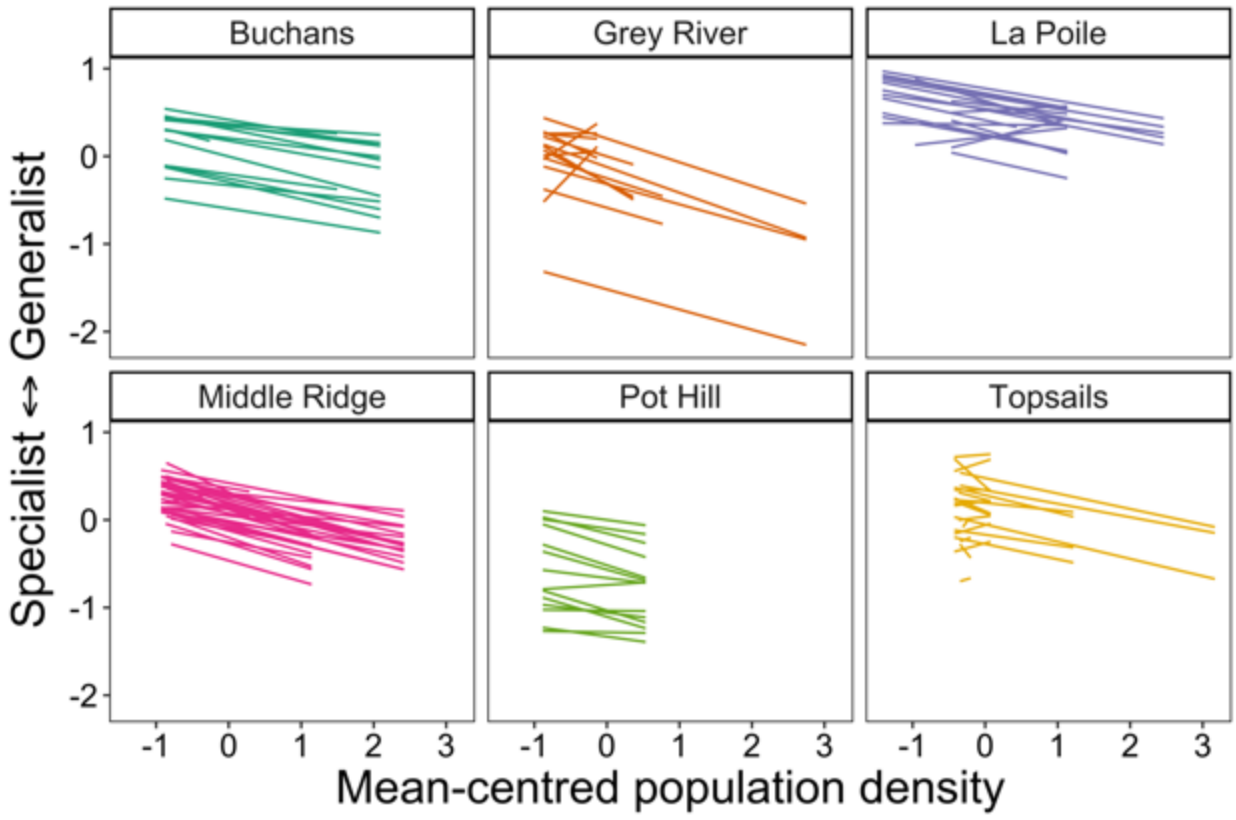

Figure S6.8: Behavioural reaction norms testing the relationship between habitat specialization and population density for caribou (*Rangifer tarandus*; n = 127) in six herds in Newfoundland. Each line represents an individual behavioural response to changes in population density and crossing of lines represents individual differences in plasticity (i.e., an individual-environment interaction).

References

Aplin LM, Farine DR, Morand-Ferron J, Sheldon BC (2012) Social networks predict patch discovery in a wild population of songbirds. Proc R Soc B Biol Sci 279:4199–4205. doi: 10.1098/rspb.2012.1591

Bastille-Rousseau G, Schaefer JA, Mahoney SP, Murray DL (2013) Population decline in semi-migratory caribou (Rangifer tarandus): intrinsic or extrinsic drivers? Can J Zool 91:820–828. doi: doi:10.1139/cjz-2013-0154

Bjørneraas K, Van Moorter B, Rolandsen CM, Herfindal I (2010) Screening global positioning system location data for errors using animal movement characteristics. J Wildl Manage 74:1361–1366. doi: 10.2193/2009-405

Boyce MS, Johnson CJ, Merrill EH, et al (2016) Can habitat selection predict abundance? J Anim Ecol 85:11–20. doi: 10.1111/1365-2656.12359

Brent LJN (2015) Friends of friends: Are indirect connections in social networks important to animal behaviour? Anim Behav 103:211–222. doi: 10.1016/j.anbehav.2015.01.020

Cairns SJ, Schwager SJ (1987) A comparison of association indices. Anim Behav 35:1454–1469

Charmantier A, Garant D, Kruuk LEB (2014) Quantitative genetics in the wild. Oxford University Press

Croft DP, James R, Krause J (2008) Exploring Animal Social Networks. Princeton University Press

Csárdi G, Nepusz T (2006) The igraph software package for complex network research. InterJournal Complex Syst 1695:1–9

Dingemanse NJ, Kazem AJN, Réale D, Wright J (2010) Behavioural reaction norms: animal personality meets individual plasticity. Trends Ecol Evol 25:81–89. doi: 10.1016/j.tree.2009.07.013

Dolins FL, Mitchell RW (2010) Spatial cognition, spatial perception: Mapping the self and space. Cambridge University Press

Drewe JA (2010) Who infects whom? Social networks and tuberculosis transmission in wild meerkats. Proc R Soc B 277:633–42. doi: 10.1098/rspb.2009.1775

Farine DR (2017) A guide to null models for animal social network analysis. Methods Ecol Evol 8:1309–1320. doi: 10.1111/2041-210X.12772

Farine DR (2014) Measuring phenotypic assortment in animal social networks: Weighted associations are more robust than binary edges. Anim Behav 89:141–153. doi: 10.1016/j.anbehav.2014.01.001

Farine DR, Whitehead H (2015) Constructing, conducting and interpreting animal social network analysis. J Anim Ecol 84:1144–1163. doi: 10.1111/1365-2656.12418

Fisher DN, Rodríguez-Muñoz R, Tregenza T (2016) Comparing pre- and post-copulatory mate competition using social network analysis in wild crickets. Behav Ecol 00:arv236. doi: 10.1093/beheco/arv236

Godfrey SS., Anasri TH, Gardner MG, et al (2014) A contact-based social network of lizards is

defined by low genetic relatedness among strongly connected individuals. Anim Behav 97:35–43. doi: 10.1016/j.anbehav.2014.08.019

Hadfield JD (2010) MCMC methods for multi-respoinse generalized linear mixed models: The MCMCglmm R package. J Stat Softw 33:1–22

Hinde RA (1976) Interactions, relationships and social structure. Man 11:1–17

Jacoby DMP, Papastamatiou YP, Freeman R (2016) Inferring animal social networks and leadership: applications for passive monitoring arrays. J R Soc Interface 13:20160676

Johnson CJ, Seip DR, Boyce MS (2004) A quantitative approach to conservation planning: Using resource selection functions to map the distribution of mountain caribou at multiple spatial scales. J Appl Ecol 41:238–251. doi: 10.1111/j.0021-8901.2004.00899.x

Johnson DH (1980) The comparison of usage and availability measurements for evaluating resource preference. Ecology 61:65–71. doi: 10.2307/1937156

Manly BFJ, McDonald LL, Thomas DL, et al (2002) Resource selection by animals: statistical design and analysis for field studies, 2nd Editio. Kluwer Academic, Dordrecht

McLoughlin PD, Morris DW, Fortin D, et al (2010) Considering ecological dynamics in resource selection functions. J Anim Ecol 79:4–12. doi: 10.1111/j.1365-2656.2009.01613.x

Mennill DJ, Battiston M, Wilson DR, et al (2012) Field test of an affordable, portable, wireless microphone array for spatial monitoring of animal ecology and behaviour. Methods Ecol Evol 3:704–712. doi: 10.1111/j.2041-210X.2012.00209.x

Moore AJ, Brode III ED, Wolf JB (1997) Interacting phenotypes and the evolutionary process : I. direct and indirect genetic effects of social interactions. Evolution (N Y) 51:1352–1362

Morris DW (2003) Toward an ecological synthesis: A case for habitat selection. Oecologia 136:1–13. doi: 10.1007/s00442-003-1241-4

Nakagawa S, Schielzeth H (2013) A general and simple method for obtaining R2 from generalized linear mixed-effects models. Methods Ecol Evol 4:133–142. doi: 10.1111/j.2041-210x.2012.00261.x

Ossi F, Focardi S, Picco G Pietro, et al (2016) Understanding and geo-referencing animal contacts: proximity sensor networks integrated with GPS-based telemetry. Anim Biotelemetry 4:21. doi: 10.1186/s40317-016-0111-x

Perkins SE, Cagnacci F, Stradiotto A, et al (2009) Comparison of social networks derived from ecological data: Implications for inferring infectious disease dynamics. J Anim Ecol 78:1015–1022. doi: 10.1111/j.1365-2656.2009.01557.x

Pruitt JN, Bolnick DI, Sih A, et al (2016a) Behavioural hypervolumes of spider communities predict community performance and disbandment. Proc R Soc B 283:20161409

Pruitt JN, Bolnick DI, Sih A, et al (2016b) Authorship removal correction for “Behavioural hypervolumes of spider communities predict community performance and disbandment.” Proc R Soc B Biol Sci 283:2020. doi: 10.1098/rspb.2016.1409

Robitaille AL, Webber QMR, Vander Wal E (2019) Conducting social network analysis with animal telemetry data: applications and methods using spatsoc. Methods Ecol Evol 10:1203–1211. doi: 10.1111/2041-210X.13215

Saltz JB, Geiger AP, Anderson R, et al (2016) What, if anything, is a social niche? Evol Ecol 30:349–364. doi: 10.1007/s10682-015-9792-5

Seyfarth RM, Cheney DL (2015) Social cognition. Anim Behav 103:191–202. doi: 10.1016/j.anbehav.2015.01.030

Sih A, Bell AM, Johnson JC, Ziemba ARE (2004) Behavioural syndromes: an integrative overview. Q Rev Biol 51:211–44

Sikes RS, Mammalogists AC and UC of the ASO (2016) 2016 Guidelines of the American Society of Mammalogists for the use of wild mammals in research and education. J Mammal 97:663–688. doi: 10.1093/jmammal/gyw078

Spiegel O, Leu ST, Sih A, Bull CM (2016) Socially interacting or indifferent neighbours? Randomization of movement paths to tease apart social preference and spatial constraints. Methods Ecol Evol 7:971–979. doi: 10.1111/2041-210X.12553

Trainor AM, Schmitz OJ (2014) Infusing considerations of trophic dependencies into species distribution modelling. Ecol Lett 17:1507–1517. doi: 10.1111/ele.12372

Vandeperre F, Aires-da-Silva A, Lennert-Cody C, et al (2016) Essential pelagic habitat of juvenile blue shark (Prionace glauca) inferred from telemetry data. Limnol Oceanogr 61:1605–1625. doi: 10.1002/lno.10321

Vander Wal E, Yip H, McLoughlin PD (2012) Sex-based differences in density-dependent sociality: An experiment with a gregarious ungulate. Ecology 93:206–212. doi: 10.1890/11-0020.1

Whitehead H (2008) Analyzing animal societies: quantitative methods for vertebrate social analysis. University of Chicago Press